



Hawai‘i Pacific University

POPULATION SIZE AND STRUCTURE OF MELON-HEADED WHALES (*PEPONOCEPHALA ELECTRA*) AROUND THE MAIN HAWAIIAN ISLANDS: EVIDENCE OF MULTIPLE POPULATIONS BASED ON PHOTOGRAPHIC DATA



by

Jessica M. Aschettino

May 14, 2010

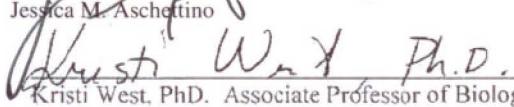
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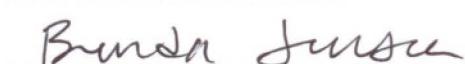
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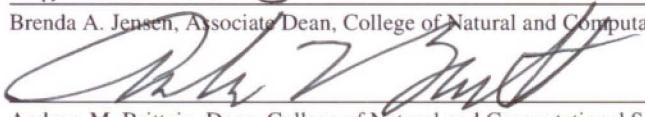
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Abstract

Despite the presence of melon-headed whales in tropical and sub-tropical waters worldwide, little is known about this species. Melon-headed whales frequent offshore waters surrounding the Main Hawaiian Islands where aerial surveys by Mobley and colleagues suggest a relatively small population (154 individuals ($CV=0.88$)). A 2004 near mass-stranding in Hanalei Bay, Kaua‘i occurred when an embayment of 150 – 200 animals coincided with naval mid-frequency sonar use. To assess population size and movements in Hawai‘i, more than 40,000 photos were collected from 47 encounters around the Main Hawaiian Islands between 2002 and 2009, and additional photos were obtained from collaborators from 1986 – 2001. Using only good quality photographs, there were 1,433 unique individuals in the photo-identification catalog, of which 1,046 were distinctive. Of these, 330 (31.5%) were seen on more than one occasion. Re-sighting data combined with social network analyses showed evidence of two distinct populations – a smaller, resident population, seen exclusively off the northwest region of the island of Hawai‘i, and a much larger Main Hawaiian Islands population, seen throughout the entire range of the Main Hawaiian Islands. Depth of encounters with the resident population were significantly shallower (median = 381 m) than those with the Main Hawaiian Island population (median = 1,844 m). Re-sightings of individuals have occurred up to 22 years apart for the Hawai‘i resident population and up to 13 years apart for the Main Hawaiian Islands population, suggesting long-term residency for both populations. Dorsal fin disfigurements suggest that fisheries interactions occur with members of both populations. Abundance estimated through mark-recapture analyses (corrected for the non-distinctive individuals), was 447 ($CV = 0.12$) for the Hawai‘i residents and 5,794 ($CV = 0.20$) for the Main Hawaiian Islands population. These estimates provide more accurate and precise population estimates of melon-headed whales in Hawai‘i. Although the total population size of melon-headed whales in

Hawai‘i is higher than once believed, the restricted range of the small resident population may pose additional management implications for these individuals.

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Chapter One

Literature Review

*The Melon-Headed Whale (*Peponocephala electra*)*

Despite the presence of melon-headed whales (*Peponocephala electra*) in tropical and subtropical waters worldwide, very little is known about this delphinid species. The melon-headed whale was originally identified in Hawai‘i. The first account of the species is from Hilo Bay, Hawai‘i in 1841 where approximately 60 animals were driven ashore and harvested for their meat and oil (Wilkes 1845). According to Wilkes, “the moment a school of porpoises is discovered, it is their usual practice to drive them in” referring to native Hawaiians. This drive fishery is contrary to some beliefs that native Hawaiians held dolphins to be sacred and did not hunt them. From a specimen of this drive, the species was described by Peale (1848), who named them *Phocaena pectoralis*; however it was Gray (1846), who is more commonly credited with the discovery of the species and subsequently provided the scientific name, *Lagenorhynchus electra* (Gray 1846) (Figure 1.1).

The species has undergone several changes to both its scientific and common name since its initial discovery, but in 1966 the species underwent its most recent reclassification when Nishiwaki and Norris (1966) determined that they were unique enough from other species of the genus *Lagenorhynchus*, to be placed in their own, *Peponocephala*. At the time, the authors believed the Latin prefix *pepo* translated into “melon”; however, cetologist Dale Rice later revealed that the literal translation of the word is actually “pumpkin” (Reeves et al. 2002). The most widely used common name, melon-headed whale, comes from the species’ blunt rostrum and rounded head, which appears almost triangular when viewed from the side or above. Other vernacular names include blackfish (although this is also used for several other species), electra

dolphin, many-toothed blackfish, Hawaiian blackfish, Hawaiian porpoise, and the Indian broad-beaked dolphin (Nishiwaki and Norris 1966, Perrin 1976, Shallenberger 1981, Perryman 1994, Jefferson and Barros 1997). The species is mostly dark gray in color and white pigmentation is common around the mouth (Jefferson and Barros 1997). A faint, but darker gray dorsal cape is present, along with a broad dark eye band or patch that gives the appearance of the animal wearing a mask (Perryman 2009). Lighter gray regions are common on the ventral side and the pectoral fins are sharply pointed (Figure 1.2). Some sexual dimorphism exists between the sexes: males tend to be slightly longer (about 2.5 m compared to about 2.4 m for females), more robust, and have longer pectoral flippers, taller dorsal fins, rounder heads, and wider tail flukes than females (Best and Shaughnessy, 1981, Miyazaki et al. 1998, Perryman 2009). Additionally, a pronounced ventral keel posterior to the anus is present in adult males (Miyazaki et al. 1998, Perryman 2009) (Figure 1.1). Maximum weight is around 225 kg (Reeves et al. 2002), although mean weight from 119 animals that stranded in Japan in 1982 was calculated to be about 200 kg for males and 161 kg for females (Miyazaki et al. 1998). From this same stranding event, 74 animals were examined for age composition using dental or cemental growth layers in the teeth. Females ranged from 5.5 – 44.5 years, and males ranged from 2.5 – 38.5 years. Sexually mature females were found to be between 11.5 and 44.5 years of age, and possibly sexually mature males (those having a testis weight of 200g or more) were between 16.5 and 38.5 years of age. The oldest pregnant female was 41.5 years, and it is possible female melon-headed whales do not undergo reproductive senescence, as has been suggested for some species of odontocetes, including short-finned pilot whales (*Globicephala macrohynchus*) (Marsh and Kasuya 1984) and killer whales (*Orcinus orca*) (Olesiuk et al. 1990).

Melon-headed whales are sometimes confused with false killer whales (*Pseudorca crassidens*), but most often with pygmy killer whales (*Feresa attenuata*) (Jefferson and Barros 1997). All three species have a similar dark body, rounded heads, falcate fins, and all appear to inhabit the same oceanic regions (Watkins et al. 1997). These three species, combined with the short-finned pilot whale in Hawai‘i, make up a group of odontocetes commonly referred to as the “blackfish.” When sighted, melon-headed whales have frequently been seen associating with other species, including rough-toothed dolphins (*Steno bredanensis*) in the Mariana Islands (Jefferson et al. 2006), French Polynesia (Gannier 2000), and the Gulf of Mexico (Mullin 1994), Risso’s dolphins (*Grampus griseus*) in Taiwan (Wang et al. 2001) and Fraser’s dolphins (*Lagenodelphis hosei*) in Micronesia (Eldredge 1991), French Polynesia (Gannier 2000), the Philippines (Dolar et al. 2006), the Gulf of Mexico (Mullin 1994), and the Eastern Tropical Pacific (Wade and Gerrodette 1993). In Hawai‘i, sightings with other species have also been documented and include short-finned pilot whales (Migura and Meadows 2002, Huggins et al. 2005), pygmy killer whales (Barlow 2006), humpback whales (*Megaptera novaeangliae*), pantropical spotted dolphins (*Stenella attenuata*), rough-toothed dolphins, and killer whales (Huggins et al. 2005).

Melon-headed whales often appear in relatively large groups, frequently numbering 500 or more animals (Shallenberger 1981), although smaller groups are occasionally seen with 20 or fewer individuals (Eldredge 1991, Huggins et al. 2005). Mean group size from 14 sightings in the Eastern Tropical Pacific (ETP) was nearly 200 (CV = 0.20) (Wade and Gerrodette 1993). Group size from nine encounters around Mayotte in the Mozambique Channel Islands ranged from 140 – 450 (mean = 288, SD = 84) (Kiszka et al. 2008). In the Marquesas Islands mean group size from 14 encounters was 85 individuals (variance not reported) (Gannier 2002), and in

Hawai‘i, group size ranged from 17 – 800 individuals (mean = 304, SD = 189, n = 18) (Huggins et al. 2005). Jefferson and Barros (1997) suggest that strong social bonds exist, based on their tendency to mass-strand, although the intricacies of their social behavior have not been examined. Social structure has been described for many odontocetes, and ranges from stable pods, as seen in fish-eating killer whales in Greater Puget Sound (Balcomb et al. 1982) to highly variable schools, as seen in spinner dolphins in the Main Hawaiian Islands (Norris and Dohl 1980). Although not an exact index, group stability may become increasingly fluid in the smaller odontocetes (Bräger 1999).

Captive rearing and maintenance of melon-headed whales has been unsuccessful with the exception of a handful of rehabilitated animals and individuals housed at Sea Life Park, Hawai‘i over several years. One individual at Sea Life Park was described as exhibiting aggressive behavior towards both trainers and other tank mates (Anonymous 2005) and Shallenberger (1981) depicts instances of aggression towards humans from both captive and wild animals.

Day-time behavior for melon-headed whales in Hawai‘i, along with several other oceanic island groups (e.g. Palmyra Atoll, Rota, and the Marquesa islands of French Polynesia), often involves resting/logging at the surface (Brownell et al. 2009). Such behavior may be suggestive of nighttime feeding, as seen with spinner dolphins in Hawai‘i who rest during the day and feed on a vertically migrating prey layer at night (Benoit-Bird et al. 2003). Acoustic monitoring of melon-headed whales at Palmyra Atoll also suggests, based on an increase in echolocation clicks at night, that foraging is predominantly occurring at night (Baumann-Pickering 2009). Although relatively few stomach contents have been analyzed, melon-headed whales are believed to feed primarily on pelagic and mesopelagic fish and squid (Best and Shaughnessy 1981, Sekiguchi et al. 1992, Jefferson and Barros 1997). The stomach contents of

one individual that stranded on O‘ahu consisted primarily of squid beaks, although determination of species is awaiting analysis (West unpublished). Stomachs of 21 individuals who perished in a mass stranding event at Piracanga Beach, Bahia, Brazil were examined for food remains. Contents were found in 18 of these, with squid from eight families represented, and a myctophid fish (sp. *Lampadena*) accounting for 95.4% of otoliths found (Barros et al. 1990). In Hawai‘i, all eight squid families (Roper and Young 1975), as well as the myctophids (Clarke 1978) are known to undergo diel vertical migrations, with some species ascending to depths of 200 m or less at night; therefore, it seems plausible that during the daytime, melon-headed whales may decrease their activity in association with resting behavior and become increasingly active at night, coinciding with feeding.

Natural predation on melon-headed whales is likely to occur from large sharks and killer whales. Non-lethal injuries from cookie cutter sharks (*Isitius brasiliensis*) are evident on both free-ranging (Figure 1.3) and stranded animals (Best and Suaughnessey 1981, Gasparini and Sazima 1996, Miyazaki et al. 1998). While there is no one leading conservation issue that has been identified for melon-headed whales, various threats do exist. Individuals are taken in small numbers in subsistence, drive, and harpoon fisheries in several locations worldwide, including Japan, Taiwan, and Indonesia (Nishiwaki and Norris 1966, Taylor et al. 2008). They are taken incidentally in the tuna purse seine fishery (Perrin 1976) and may also be injured or killed through interactions with other fisheries. It has been suggested that the most direct threat to marine mammal species on a global scale is incidental mortality in fishing gear (Kiszka et al. 2008). Interactions with fisheries has been one of the suggested causes of a dramatic decline in abundance of false killer whales around the Main Hawaiian Islands (Baird 2009, Reeves et al. 2009), first evident from photographic data of dorsal fin disfigurements (Baird and Gorgone

2005). Dorsal fin disfigurements and other injuries indicative of fishery interactions are also apparent from individual melon-headed whales near Mayotte, in the Mozambique Channel Islands (Kiszka et al. 2008), Palmyra Atoll (Pitman pers comm.), and Hawai‘i (Chapter 2). While vessel collisions pose serious risks for some marine mammal species, a global assessment of vessel collisions on small odontocetes failed to find any evidence of collisions with melon-headed whales (Van Waerebeek et al. 2007), although at least one individual from Hawai‘i has injuries that may be from a propeller (Chapter 2). Finally, although difficult to quantify their effects, decreasing food sources, linked to both overfishing and climate change, may become two increasingly important conservation topics for this, and other species.

Mass Strandings and Anthropogenic Noise

A stranded animal is defined as an individual who has come ashore, but can also refer to an animal that is outside its normal habitat, or “survival envelope” (Geraci and Lounsbury 2005). Mass strandings typically refer to two or more animals of the same species coming ashore (with the exception of a mother-calf pair) at the same time and place. While both odontocetes and mysticetes may strand, it is the highly social odontocetes that typically mass strand. Mass strandings of melon-headed whales often involve hundreds of animals (Lodi et al. 1990), and there are at least 33 known occurrences of such events worldwide (Brownell et al. 2009). Twenty two strandings of melon-headed whales have occurred around the Main Hawaiian Islands since 1955 (NMFS stranding database¹). If the 1841 event, in which approximately 60 animals were driven ashore, is included (Wilkes 1845)—which can be argued as the animals were close enough to shore to have been driven in by canoes—then this number increases to at least 23 strandings since 1841. Sixteen of these occurred on O‘ahu, three on Maui, two on

¹ Available from Pacific Islands Regional Office, 1601 Kapi‘olani Blvd. Suite 1110, Honolulu, HI 96814

Kaua‘i, and one on Hawai‘i (two when including the 1841 event). Excluding the 1841 event, two mass strandings have occurred in the Main Hawaiian Islands; one on O‘ahu (two animals in 2003) and one on Kaua‘i (150—200 animals in 2004). There are a number of theories as to why mass strandings occur, including individuals following an impaired animal ashore, disease, parasites, bottom topography, tidal change, and the influence of sonar or other anthropogenic noise. The latter has received increasing attention in recent years due to certain species of deep-diving odontocetes, such as beaked whales, appearing susceptible to solitary or mass stranding events in response to high-intensity sonar (e.g., Balcomb and Claridge 2001). Mid-frequency sonar use may elicit behavioral modification and may also cause underlying physiological responses, and a number of mass strandings have been shown to correlate in space and time with such sonar use (Cox et al. 2006).

In July of 2004, between 150 and 200 melon-headed whales entered the shallow waters of Hanalei Bay, Kaua‘i coincident with active mid-frequency sonar use during the biennial Rim of the Pacific (RIMPAC) naval training exercise (Southall et al. 2006). Melon-headed whales around the Main Hawaiian Islands have shown a preference for deep, offshore waters, ranging from 148 – 4,779 m (median =1,610 m) (Ligon et al. 2007). Bottom depth at Hanalei Bay is 20 m or less, with an average depth of 10 m; therefore, this embayment was clearly an example of the animals being outside of their normal habitat, and consequently was classified as a mass stranding (Southall et al. 2006). The animals spent over 28 hours in the bay and were observed swimming in tight circles before eventually being herded out of the bay with human assistance (Figure 1.4). A lone neonatal calf was the only known casualty, and a subsequent necropsy suggested cause of death was poor nutritional status. An extensive report of the embayment

concluded that the use of mid-frequency sonar was a “plausible, if not likely, contributing factor” (Southall et al. 2006).

On the same day, some 5,700 km away, another aggregation of approximately 500 – 700 melon-headed whales was observed at Sasanhaya Bay, Rota, in the Northern Mariana Islands (Jefferson et al. 2006). The authors described observations of these animals during the five and a half hour encounter, which included behaviors such as bowriding and “penis extrusions.” The encounter began in waters that would be considered shallow for the species, 77 m (although few reports exist at all for this region, and observations from Palmyra Atoll have been reported at depths as shallow as 100 m; Brownell et al. 2009), but ended in waters with a bottom depth of 1,100 m (Jefferson et al. 2006). While the circumstances and behaviors of animals at these two locations were very different, some have argued that the two events may be connected (Mobley et al. 2007). These critics have suggested lunar cycles, not sonar, may have been responsible for the embayment of melon-headed whales on Kaua‘i and for the presence of animals at Rota. Brownell et al. (2009) examined and contrasted these two events, as well as two additional sightings of melon-headed whales at Hatiheu Bay, Nuku Hiva. Furthermore, they examined all records of mass stranding events of melon-headed whales where date was known ($n = 23$) in order to assess whether moon phases were a likely contributor to these events. Their results showed that lunar cycles and mass stranding events were not, in fact, correlated.

Another unusual mass stranding event took place in Antsohihy Bay, Madagascar in May of 2008. Between 100 – 200 melon-headed whales stranded in a complex system of intertidal waterways while hydrocarbon industry exploration by Exxon-Mobil was occurring offshore (Rosenbaum et al. 2009). At least 60 deaths were reported, and the possibility of unreported or unknown deaths is also likely given the intricacies of the mangrove habitat in which the

stranding took place. While this incident is still under investigation, both this and the Hanalei Bay event are suggestive of melon-headed whales' potential vulnerability to anthropogenic noise. It is therefore important to determine biological parameters such as accurate estimates of population sizes, home ranges, and habitat preferences for this species in order to assess threats and to develop management plans aimed at protecting known populations.

Population Status

Knowledge of population size and structure is important in the management of any cetacean population. Although melon-headed whales are listed as 'least concern' on the IUCN Red List of Threatened Species (Taylor et al. 2008), only a handful of abundance estimates are available from any region of the world, and hence no population trend data exists for the species. Without such monitoring, it is impossible to evaluate whether stocks are declining, increasing, or remaining constant. The available abundance estimates for melon-headed whales were obtained from line transect surveys. Abundance in the northern Gulf of Mexico is estimated at 3,451 (CV = 0.55) (Mullin and Fulling 2004). Dolar et al. (2006) provided estimates in the Philippines; for the eastern Sulu Sea the abundance estimate is 921 (CV = 0.82) and the estimate in the Tañon Strait is 1,383 (CV = 0.82). Wade and Gerrodette (1993) have estimated the melon-headed whale population for a large portion of the ETP (an area of 19,148,000 km²) at 45,400 (CV = 0.47) individuals. A 2002 line-transect vessel survey that included the entire Hawaiian Island chain extending out to the Hawaiian Exclusive Economic Zone (EEZ), a region that includes out to 370 km from shore, generated an abundance estimate of 2,950 (CV = 1.17) (Barlow 2006). This survey, however, is based on the observation of only one group of melon-headed whales,

and because of this, results from other studies, i.e. covariates, from 1986-2002 surveys, were also used in order to estimate population size.

Until recently, the only abundance estimate available around the Main Hawaiian Islands was 154 individuals ($CV = 0.88$), based on aerial surveys conducted between 1993 and 1998 (Mobley et al. 2000). This study focused on odontocete sightings within approximately 46 km of the Main Hawaiian Islands and the abundance estimate was based on only three sightings of melon-headed whales. Shallenberger (1981) states that “a small pod of 75-150 animals has been consistently observed off the North Kohala Coast, Hawai‘i.” While this last statement is based more on anecdotal sightings (and is now nearly 30 years old), both of the abundance estimates (Barlow 2006, Mobley et al. 2000) have high variance, suggesting the need for greater accuracy in estimates of population size of melon-headed whales around the Main Hawaiian Islands. In order to assess the status of this species in Hawai‘i, Huggins et al. (2005) initiated a photo-identification catalog of melon-headed whales and documented 338 distinctive individuals. This catalog has grown to 1,046 distinctive individuals (Chapter 2), shedding new light on population size, population structure, and movements of melon-headed whales around Hawai‘i.

Photo-Identification and Mark-Recapture

In simple terms, the theory of mark-recapture (or capture-recapture) is merely a ratio between known and unknown values (Manly et al. 2005). Early uses of this method date back to the 1600s, when John Graunt attempted to estimate population sizes and the effect of the plague in England (Hald 2003), and while models have evolved, the basic principle remains the same. Physical marking of animals through the use of tags, bands, or other means, is a popular way for avian and terrestrial biologists to use mark-recapture techniques to estimate life history

parameters on their respected subjects. Natural markings also provide a means to monitor individuals, and may even be superior to physically marking, as animals are not required to be handled or manipulated.

Such natural markings are present on many marine mammal species. When photographed, the natural markings on dorsal fins and/or tail flukes of cetaceans provide a way to identify individual animals again in the future. For many species of cetaceans, and especially dolphins, the trailing edge of the dorsal fin is the most identifying feature (Würsig and Jefferson 1990). Patterns and notches on the trailing edge can be used to identify individuals as being distinct (Hammond 1986, Wells and Scott 1990). Due to these unique qualities, the animals can then be classified as “marked.” Any animal photographed and recognized again in the future is then classified as “recaptured.” Such photo-identification (photo-id) studies have become increasingly valuable with respect to marine mammal research, and among other parameters, have proven successful for estimating population sizes for many species.

The theory behind basic mark-recapture modeling is that the number of marked animals that are recaptured in a sample will be equivalent to the proportion of marked animals in the total population (Hammond 1986). A widely used and rather basic representation is the Petersen-Lincoln estimator, after Petersen (LeCren 1965) and Lincoln (1930):

$$N = \frac{MC}{R} \quad (1.1)$$

Where N is the estimated population size, M is the number of marked animals captured on the first occasion, C is the number of animals captured on the second occasion, and R is the number of marked individuals that were recaptured between the first and second occasion. Petersen-Lincoln estimators are based on only two encounter occasions. Seber (1982) suggests a slightly modified version of the above formula to reduce bias in the population estimate:

$$N = \frac{(M + 1)(C + 1)}{R + 1} - 1 \quad (1.2)$$

Numerous models exist for such analyses and are available for both closed and open populations.

Closed population analyses generally assume that populations are closed to births, deaths, immigration, and emigration, whereas open populations assume individuals may enter and leave the population (through any of the above processes) between sampling periods. The Petersen-Lincoln estimator assumes a closed population, and while closed populations are more straightforward to model, it may be more difficult to meet their assumptions. To examine the population of melon-headed whales around the Main Hawaiian Islands using multi-year data, the assumptions of a closed population are violated, and therefore an open population model should be employed. The open population model that is most widely used is the Jolly-Seber model (Pollock and Alpizar-Jara 2005) from Jolly (1965) and Seber (1965). The model assumes the following (modified from Seber 1982):

1. Every animal in the population, whether marked or unmarked, has the same probability of being “caught” (i.e. photographed) in a given sample, assuming that it is alive and in the population when the encounter occurs.
2. Every marked animal has the same probability of surviving from one encounter to another, and of being in the population at the time of the subsequent encounter, given that it is alive and in the population immediately after the initial encounter.
3. Every animal caught in a given encounter has the same probability of being returned to the population.
4. Marked animals do not lose their marks, and all marks are recorded from each encounter
5. All encounters are instantaneous.

Jolly-Seber abundance estimates can be made using a variety of modeling programs.

Program MARK v 6.0 (White and Burnham 1999) estimates population parameters using

maximum likelihood techniques. There are a number of modeling packages within MARK, each with its own specialization. The modeling program POPAN (Schwarz and Arnason 1996), is the most capable software for the analysis of population size. POPAN has been used to estimate population size of many marine, terrestrial, and avian species. Population size has been estimated using POPAN in several recent studies on humpback whales (*Megaptera novaeangliae*) (Larsen and Hammond 2004), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Reisinger and Karczmarski 2009), and the Australian snubfin dolphin (*Orcaella heinsohni*) and Indo-Pacific humpback dolphins (*Sousa chinensis*) (Parra et al. 2006).

One goal of early cetacean mark-recapture work was to assess large whale stocks following the intensive whaling era (e.g. Tillman and Mizroch 1982). While studies evolved to incorporate the estimation of other parameters, including births, deaths, immigrations, and emigrations, abundance estimates continue to be a widely sought after goal of mark-recapture work. Studies have ranged from relatively short durations (e.g. one year/field season) to long-term, multi-year efforts. While smaller populations may be examined over short durations, larger populations require increased efforts. Long-term datasets are preferable in that population estimates become more precise and less biased (Hammond 1990).

The longest-running study of an odontocete population is the Sarasota Dolphin Research Program (SDRP), which has, for nearly 40 years, studied bottlenose dolphin populations in Sarasota Bay, Florida (e.g. Wells and Scott 1990). This work commenced in 1970 when researchers began identifying individual bottlenose dolphins in the Sarasota Bay area through photographs and markings that were given to the animals during catches. Due to the longevity of this research, and the small number of individuals in the population (about 100), this is one of the best known populations anywhere in the world. Mark-recapture work has expanded significantly

since such early projects, and has now been done on a multitude of cetaceans—ranging in size and habitat preference—such as common bottlenose dolphins (Baird et al. 2001), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Reisinger and Karczmarski 2009), humpback whales (Calambokidis et al. 2001, 2008), sperm whales (*Physeter macrocephalus*) (Whitehead 2001), long-finned pilot whales (Auger-Méthe and Whitehead 2007), and Hector’s dolphins (*Cephalorhynchus hectori*) (Gormley et al. 2005). One of the largest, and most comprehensive photo-identification projects undertaken was SPLASH (Structure of Populations, Levels of Abundance, and Status of Humpbacks), which, as the acronym suggests, was aimed at determining the population structure, abundance, trends, movements, and the effect of humans, on humpback whales inhabiting the North Pacific (Calambokidis et al. 2008). Vast migrations by the species required a highly collaborative effort by more than 50 research organizations to effectively estimate the desired parameters. Throughout only three field seasons (2004, 2005, and 2006) nearly 8,000 unique individual humpback whales were included in the SPLASH catalog and the best estimate of abundance was more than 18,000 individuals (Calambokidis et al. 2008). Mark-recapture studies clearly have a wide application, and current methods provide a relatively non-invasive way to estimate abundance of a wide variety of cetacean species.

Site Fidelity

Site fidelity is an important issue in determining habitat use and home range for species. Site fidelity refers to the tendency of an individual to return to an area previously occupied, or to remain in an area over an extended period (Baird et al. 2008a). Evidence of island-associated populations exists for common bottlenose dolphins off the Bermuda Pedestal (Klatsky et al. 2007), and in recent years, dedicated research and photographic evidence of Hawaiian

odontocetes has determined that many species exhibit island-association. For example, rough-toothed dolphins (Baird et al. 2008a), common bottlenose dolphins (Baird et al. 2009), spinner dolphins (Norris et al. 1994, Andrews et al. 2006), pygmy killer whales (McSweeney et al. 2009), false killer whales (*Pseudorca crassidens*) (Baird et al. 2008b), Cuvier's beaked whales (*Ziphius cavirostris*), and Blainville's beaked whales (*Mesoplodon densirostris*) (McSweeney et al. 2007) all show evidence of site fidelity. Melon-headed whales at Palmyra Atoll and Nuku Hiva, French Polynesia (Brownell et al. 2009) have demonstrated some evidence of island-association. Huggins et al. (2005) also showed some site fidelity for melon-headed whales in Hawai'i via photographic re-sighting data, and Schorr et al. (2009) documented movements of melon-headed whales between the Main Hawaiian Islands through the use of satellite tags. Range of movements from the satellite tagging data was highly variable. During a 25-day period (the maximum length of time a tag was deployed), one individual stayed within 50 km of where it was tagged, whereas another individual moved 559 km in just nine days (Schorr et al. 2009). It is possible that melon-headed whales in Hawai'i are following short term oceanographic features, such as fronts and eddies, which could account for the vast discrepancies between individual satellite tracks (Woodworth et al. *Submitted*). Additionally, there may be different groups of melon-headed whales utilizing adjacent areas; some that are residents and stay within a small range, and others that are more transient in nature and frequently move through the range. If the animals are, in fact, primarily utilizing the entire Main Hawaiian Islands as their "home range," they would be exhibiting site fidelity over quite a significant area (~600 km). Satellite data has the advantage of showing fine scale movements over a short period of time (i.e., days to weeks). The photographic data, however, has the ability to show long-term residency, as well as confirm between-island movements. It also has the potential to show associations of different

groups of animals. Although information gained from the telemetry data is invaluable to our overall understanding of melon-headed whales in Hawaiian waters, a long-term photo-identification catalog provides additional opportunities to address questions that cannot be answered using telemetry alone.

This study utilizes a multi-year photo-identification catalog, consisting of more than 30,000 photographs, to assess population size, structure, and movements of melon-headed whales around the Main Hawaiian Islands.

Table and Figures

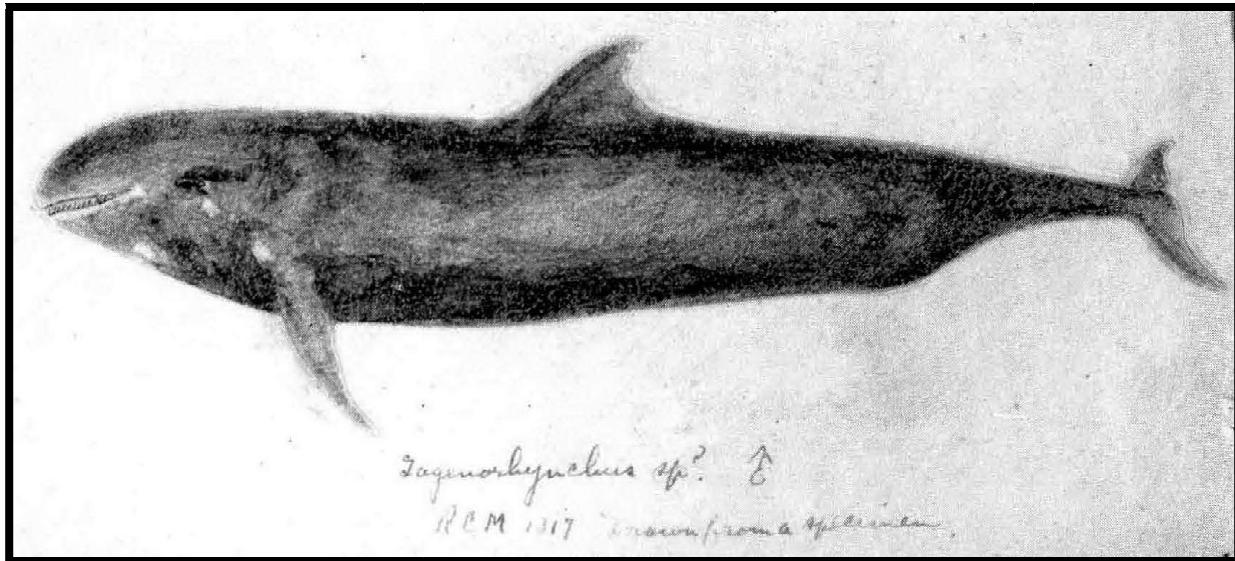


Figure 1.1 Sketch of a male melon-headed whale when the species was first described in the genus *Lagenorhynchus*. Note the pronounced ventral keel. Sketch by Robert Cushman Murphy, from Walker et al. (1945).



Figure 1.2 Melon-headed whales off the island of Hawai‘i. From the animal in the foreground, characteristic pointed pectoral flippers are seen, along with a dark eye band, white pigmentation around the lips, and lighter gray ventral region. Also noteworthy are the rounded healed scars, likely from cookie cutter shark bites (*Isistius brasiliensis*). Background animals show typical falcate dorsal fins. Photo ©Cascadia Research Collective, Daniel Webster.



Figure 1.3 Free ranging melon-headed whale (catalog no. HIPe0677) in Hawai‘i with open wound on peduncle from a cookie cutter shark (*Isistius brasiliensis*). This injury is known to be non-lethal – the animal was re-sighted one and three years later. Cookie cutter scars are common and form lighter circular or half-moon shaped scars (also faintly evident on this individual). Photo ©Cascadia Research Collective; Erin Falcone.



Figure 1.4 Melon-headed whales swimming in tight circle after entering the shallow waters of Hanalei Bay, Kaua‘i, July 3, 2004. Photo ©Gretchen Johnson.

Literature Cited

- Andrews, K.R., Karczmarski, L., Au, W.W.L., Richards, S., Vanderlip, C.A., Toonen, R.J. 2006. Patterns of genetic diversity of the Hawaiian spinner dolphin (*Stenella longirostris*). Atoll Research Bulletin 543: 65-73.
- Anonymous. 2005. Whales, Dolphins, and Porpoises: Presentation of the Cetaceans. Aquatic Mammals 31(3): 288-310.
- Auger-M'ethe', M. and Whitehead, H. 2007. The use of natural markings in studies of long-finned pilot whales (*Globicephala melas*). Marine Mammal Science 23: 77-93.
- Baird, R.W., Gorgone, A.M., Ligon, A.D., Hooker, S.K. 2001. Mark-recapture abundance estimate of bottlenose dolphins (*Tursiops truncatus*) around Maui and Lana'i, Hawai'i, during the winter of 2000/2001. Report prepared under contract 40JGNFO-00262 to the Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, California.
- Baird, R.W. and Gorgone, A.M. 2005. False killer whale dorsal fin disfigurements as a possible indicator of long-line fishery interactions in Hawaiian waters. Pacific Science 59: 593-601.
- Baird, R.W., Webster, D.L., Mahaffy, S.D., McSweeney, D.J., Schorr, G.S., Ligon, A.D. 2008a. Site fidelity and association patterns in a deep-water dolphin: rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian Archipelago. Marine Mammal Science 24: 535-553.
- Baird, R.W., Gorgone, A.L., McSweeney, D.L., Salden D.R., Deakos M.H., Ligon A.D., Schorr, G.S., Barlow, J., Mahaffy, S.D. 2008b. False killer whales (*Pseudorca crassidens*) around the Main Hawaiian Islands: long-term site fidelity, inter-island movements, and association patterns. Marine Mammal Science 24: 591-612.
- Baird, R.W. 2009. A review of false killer whales in Hawaiian waters: biology, status, and risk factors. Report prepared for the U.S. Marine Mammal Commission under Order No. E40475499.
- Balcomb, K.C. III and Boran, J.R., Heimlich, S.L. 1982. Killer whales in Greater Puget Sound (*Orcinus orca*). Reports of the International Whaling Commission 32: 681-685.
- Balcomb, K.C. III and Claridge, D.E. 2001. A mass stranding of cetaceans caused by naval sonar in the Bahamas. Bahamas Journal of Science 5: 2-12.
- Barlow, J. 2006. Cetacean abundance in Hawaiian waters estimated from a summer/fall survey in 2002. Marine Mammal Science 22: 446-464.
- Barros, N.B., Klages, N., Lodi, L., Siciliano, S. 1990. O encalhe em massa de golfinhos cabeca-de-melao (*Peponocephala electra*) em Itacare, Bahia, Brasil: Habitos alimentares. In

Abstracts of el 4th Reunion de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Valdivia, Chile, 12 – 15 November 1990.

Benoit-Bird, K.J. and Au, W.W.L. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology* 53: 364-373.

Best, P.B. and Shaughnessy, P.D. 1981. First record of the melon-headed whale, *Peponocephala electra*, from South Africa. *Annals of the South African Museum* 83: 33-47.

Bräger, S. 1999. Association patterns in three populations of Hector's dolphin, *Cephalorhynchus hectori*. *Canadian Journal of Zoology* 77: 13-18.

Brownell, R.J., Ralls, K., Baumann-Pickering, S., Poole, M.M. 2009. Behavior of melon-headed whales near oceanic islands. *Marine Mammal Science* 25: 639-658.

Calambokidis, J., Steiger, G.H., Straley, J.M., Herman, L.H., Cechio, S., Salden, D.R., Urban R., Jacobsen, J.K., Ziegesar, O.V., Balcomb, K.C., Gabriele, C.M., Dahleim, M.E., Uchida, S., Ellis, G., Miyamura, Y., Ladron de Guevara P., P., Yamahuchi, M., Sato, F., Mizroch, S.A., Schlender, L., Rasmussen, K., Barlow, J. 2001. Movements and structure of the humpback whale in the North Pacific. *Marine Mammal Science* 17: 769-794.

Calambokidis, J., Falcone, E.A., Quinn, T.J., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Matilla, D., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urbán R., J., Weller, D., Witteveen, B.H., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggins, J., Maloney, N. 2008. SPLASH: Structure of population levels of abundance, and status of humpback whales in the North Pacific. Final report for contract AB133F-03-RP0078.

Clarke T.A. 1978. Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. *Fishery Bulletin* 76: 495-514.

Cox, T. M., Ragen, T.J., Read, A.J., Vos, E., Baird, R.W., Balcomb, K., Barlow, J., Caldwell, J., Cranford, T., Crum, L., D'Amico, A., D'Spain, G., Fernandez, A., Finneran, J., Gentry, R., Gerth, W., Gulland, F., Hilderbrand, J., Houser, D., Hullar, T., Jepson, P.D., Ketten, D., MacLeod, C.D., Miller, P., Moore, S., Mountain, D.C., Palka, D., Ponganis, P., Rommel, S., Rowles, T., Taylor, B., Tyack, P., Wartzock, D. 2006. Understanding the impact of anthropogenic sound on beaked whales. *Journal of Cetacean Research and Management* 7: 117-187.

Dolar, M.L.L., Perrin, W.F., Taylor, B.L., Kooyman, G.L., Alwava, M.N.R. 2006. Abundance and distributional ecology of cetaceans in the central Philippines. *Journal of Cetacean Research and Management* 81: 93-111.

Eldredge, L.G. 1991. Annotated checklist of the marine mammals of Micronesia. *Micronesia* 24: 317-230.

Gannier, A. 2000. Distribution of cetaceans off the Society Islands (French Polynesia) as obtained from dedicated surveys. *Aquatic Mammals* 26: 111-126.

Gannier, A. 2002. Cetaceans of the Marquesas Island (French Polynesia): distribution and relative abundance as obtained from a small boat dedicated survey. *Aquatic Mammals* 28: 198-210.

Gasparini, J.L. and Sazima, I. 1996. A stranded melon-headed whale, *Peponocephala electra*, in southeastern Brazil, with comments on wounds from the cookiecutter shark, *Isistius brasiliensis*. *Marine Mammal Science* 12: 308-312.

Geraci, J.R. and Lounsbury, V.J. 2005. *Marine Mammals Ashore: A field guide for strandings*. John E. Schmitz & Sons Inc, Sparks, MD, 2nd edition. 371 pp.

Gormley, A.M., Dawson, S.M., Slooten, E., Bräger, S. 2005. Capture-recapture estimates of Hectors dolphin abundance at Banks Peninsula, New Zealand. *Marine Mammal Science* 21: 204-216.

Gray, J.E. 1846. The Zoology of the Voyage H.M.S. Erebus and Terror under the Command of Captain Sir James Clark Ross, R.N., F.B.S. During the Years 1839 - 1843. In J. Richardson & J. E. Gray (Eds.), *Mammalia, Birds* (Vol. 1, pp. 324). London: E.W. Janson.

Hald, A. 2003. *A History of Probability and Statistics and their Applications before 1750*. Hoboken, NJ: John Wiley & Sons, Inc.

Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. *Reports of the International Whaling Commission Special Issue* 8: 253-281.

Hammond, P.S. 1990. Capturing whales on film-estimating cetacean population parameters from individual recognition data. *Mammal Review* 20: 17-22.

Huggins, J., Baird, R.W., Webster, D.L., McSweeney, D.J., Schorr, G.S., Ligon, A.D. 2005. Inter-island movements and re-sightings of melon-headed whales within the Hawaiian Archipelago. In *Abstracts of the 16th Biennial Conference on the Biology of Marine Mammals*, San Diego, CA, December 2005.

Jefferson, T.A. and Barros, N.B. 1997. *Peponocephala electra*. *Mammalian Species* 553: 1-6.

Jefferson, T.A., Fertl, D., Michael, M., Fagan, D. 2006. An unusual encounter with a mixed school of melon-headed whales (*Peponocephala electra*) and rough-toothed dolphins (*Stenella bredanensis*) at Rota, Northern Mariana Islands. *Micronesia* 38(2): 239-244.

- Jolly, H.M. 1965. Explicit estimates from capture-recapture data with both death and immigration—stochastic model. *Biometrika* 52: 225-247.
- Kiszka, J., Pelourdeau, D., Ridoux, V. 2008. Body scars and dorsal fin disfigurements as indicators of interaction between small cetaceans and fisheries around the Mozambique Channel Island of Mayotte. *Western Indian Ocean Journal of Marine Science* 7: 185-193.
- Klatsky, L. J., Wells, R.S., Sweeney, J.C. 2007. Offshore bottlenose dolphins (*Tursiops truncatus*): Movement and dive behavior near the Bermuda Pedestal. *Journal of Mammalogy* 88: 59-66.
- LeCren, E. D. 1965. A note on the history of mark-recapture estimates. *Journal of Animal Ecology* 34: 453-454.
- Ligon, A.D., Baird, R.W., Webster, D.L., McSweeney, D.J., Schorr, G.S. 2007. Habitat preferences of melon-headed whales (*Peponocephala electra*) around the Main Hawaiian Islands: Implications for interpretation of the 2004 Hanalei Bay stranding event. In Abstracts of the 17th Biennial Conference on the Biology of Marine Mammals, Society for Marine Mammalogy, Cape Town, South Africa, November/December 2007.
- Lincoln, F.C. 1930. Calculating waterfowl abundance on the basis of banding returns. In U.S. Department of Agriculture Circulation (pp. 4). Washington, D.C.: U.S. Department of Agriculture.
- Lodi, L., Siciliano, S., Capistrano, L. 1990. Mass stranding of *Peponocephala electra* (Cetacea Globicephalinae) on Piracanga Beach, Bahia, northeastern Brazil. *Scientific Reports of Cetacean Research* 1: 79-84.
- Manly, B.F.J., McDonald, T.L., Amstrup, S.C. 2005. Introduction to the Handbook. In S.C. Amstrup, T.L. McDonald & B.F.J. Manly Eds., *Handbook of Capture-Recapture Analysis* (pp. 313). Princeton, NJ: Princeton University Press.
- Marsh, H. and Kasuya, T. 1984. Change in ovaries of the short-finned pilot whales, *Globicephala macrorhynchus*, with age and reproductive activity. *Reports of the International Whaling Commission Special Issue* 6: 311-335.
- McSweeney, D.J., Baird, R.W., Mahaffy, S.D. 2007. Site fidelity, associations, and movements of Cuvier's (*Ziphius cavirostris*) and Blainvilles's (*Mesoplodon densirostris*) beaked whales off the island of Hawai'i. *Marine Mammal Science* 23: 666-687.
- McSweeney, D.J., Baird, R.W., Mahaffy, S.D., Webster, D.L., Schorr, G.S. 2009. Site fidelity and association patterns of a rare species: pygmy killer whales (*Feresa attenuata*) in the Main Hawaiian Islands. *Marine Mammal Science* 25: 557-552.
- Migura, K.A. and Meadows, D.W. 2002. Short-finned pilot whales (*Globicephala macrorhynchus*) interact with melon-headed whales (*Peponocephala electra*) in Hawaii. *Aquatic Mammals* 28: 294-297.

- Miyazaki, N., Fuhise, Y., Iwata, K. 1998. Biological analysis of a mass stranding of melon-headed whales (*Peponocephala electra*) at Aoshima, Japan. Bulletin of the National Science Museum Series A (Zoology), Tokyo 24: 31-60.
- Mobley, J.R., Spitz, S.S., Forney, K.A., Grotfendt, R., Forestell, P.H. 2000. Distribution and abundance of odontocete species in Hawaiian waters: preliminary results of 1993-98 aerial surveys. Southwest Fisheries Science Center Administrative Report LJ-00-14C.
- Mobley, J.R., Martin, S.W., Fromm, D., Nachtigall, P.E. 2007. Lunar influences as possible cause for simultaneous aggregations of melon-headed whales in Hanalei Bay, Kauai, and Sasanhaya Bay, Rota. In Abstracts of the 17th Biennial Meeting on the Biology of Marine Mammals, Society for Marine Mammalogy, Cape Town, South Africa.
- Mullin, K.D. 1994. First sightings of melon-headed whales (*Peponocephala electra*) in the Gulf of Mexico. Marine Mammal Science 10: 342-248.
- Mullin, K.D. and Fulling, G.L. 2004. Abundance of cetaceans in the oceanic northern Gulf of Mexico. Marine Mammal Science 20: 787-807.
- Nishiwaki, M. and Norris, K. S. 1966. A new genus, *Peponocephala*, for the odontocete cetacean species *Electra electra*. Scientific Reports of the Whales Research Institute Tokyo, 20: 95-100 +105pls.
- Norris, K.S., and Dohl, T.P. 1980. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fishery Bulletin 77: 821-849.
- Norris, K.S., Würsig, B., Wells, R.S., Würsig, M. 1994. The Hawaiian Spinner Dolphin. Berkeley University Press, Berkeley, CA. 408 pp.
- Olesiuk, P.F., Bigg, M.A., Ellis, G.M. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington state. Reports of the International Whaling Commission Special Issue 12: 209-243.
- Peale, T.R. 1848. United States exploring expeditions during the years 1838, 1839, 1940, 1841, 1842. Under the command of Charles Wilkes U.S.N. volume 8, Mammalia and Ornithology. Philadelphia, C. Sherman, xxv+17-388.
- Perrin, W.F. 1976. First record of the melon-headed whale, *Peponocephala electra*, in the eastern Pacific, with a summary of world distribution. Fishery Bulletin 74: 457-458.
- Perryman, W.L., Au, D.W.K, Leatherwood, S., Jefferson, T.A. 1994. Melon-headed whale *Peponocephala electra* Gray, 1846. Pages 363-386 in S. H. Ridgway and R. Harrison, eds. Handbook of Marine Mammals. Vol. 5. The First Book of Dolphins. Academic Press, London, U.K.

- Perryman, W.L. 2009. Melon-headed whale (*Peponocephala electra*). In W. F. Perrin, B. Würsig & J. G. M. Thewissen (Eds.), *Encyclopedia of Marine Mammals* (Second ed.). Burlington, MA: Academic Press.
- Pollock, K.H. and Alpizar-Jara, R. 2005. Classical open-population capture-recapture models. In S.C. Amstrup, T.L. McDonald & B.F.J. Manly (Eds.), *Handbook of Capture-Recapture Analysis* (pp. 313). Princeton, NJ: Princeton University Press.
- Reisinger, R. R. and Karczmarski, L. 2009. Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay Region, South Africa. *Marine Mammal Science* 26(1): 86-97.
- Reeves, R.R., Stewart, B.S., Clapham, P.J., Powell, J.A. 2002. National Audubon Society Guide to Marine Mammals of the World. Alfred A. Knopf, New York, NY 528pp.
- Reeves, R. R., Leatherwood, S., Baird, R. W. 2009. Evidence of a possible decline since 1989 in false killer whales (*Pseudorca crassidens*) around the Main Hawaiian Islands. *Pacific Science* 63: 253-261.
- Roper, C.F.E., and Young, R.E. 1975. Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology* 209: 51.
- Rosenbaum, H. C., Collins, T., Calle, P., McAloose, D., Touhey, K., Randriamanantsoa, B., McClave, K., Harry, Charles T., Andrianarivelo, N., Razafindrakoto, Y., Cerchio, S., Andrianarismisa, A., Brownell, Jr. R.L. 2009. The 2008 mass stranding of melon-headed whales (*Peponocephala electra*) in Madagascar: From the international response to the scientific investigation into its potential cause and lessons-learned. In Abstracts of the 18th Biennial Conference on the Biology of Marine Mammals, Society for Marine Mammalogy, Quebec, October 2009.
- Schorr, G.S., Baird, R.W., Webster, D.L., McSweeney, D.J., Hanson, M.B., Polovina, J., Andrews, R.D. 2009. Satellite tagging of melon-headed whales (*Peponocephala electra*) in Hawai‘i reveals widely dispersed movement patterns. In Abstracts of the 18th Biennial Conference on the Biology of Marine Mammals, Quebec, October 2009.
- Schwarz, C. J. and Arnason, A. N. 1996. A general methodology for the analysis of capture–recapture experiments in open populations. *Biometrics* 52: 860–873.
- Seber, G.A.F. 1965. A note on multiple recapture census. *Biometrika* 52: 248-259.
- Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. Griffin, London, 2nd edition. 654 pp.
- Sekiguchi, K., Klages, N.T.W, Best, P.B. 1992. Comparative analysis of the diets of smaller odontocetes along the coast of southern Africa. *South African Journal of Marine Science* 12: 843-861.

- Shallenberger, E.W. 1981. The Status of Hawaiian Cetaceans. Report MMC-77/23 to the Marine Mammal Commission under contract MM7ACo28, NTIS PB82-109398, 79 pp.
- Southall, B.L., Braun, R., Gulland, F.M.D., Heard, A.D., Baird, R.W., Wilkin, S.M., Rowles, T.K. 2006. Hawaiian melon-headed whale (*Peponocephala electra*) mass stranding event of July 3-4, 2004. NOAA Technical Memorandum NMFS-OPR-31.
- Taylor, B. L., Baird, R. W., Barlow, J., Dawson, S. M., Ford, J., Mead, J. G., Notarbartolo di Sciara, G., Wade, P., Pitman, R.L. 2008. *Peponocephala electra*. In: IUCN 2009. IUCN Red List of Threatened Species. Version 2009.2 <www.iucnredlist.org> (accessed February, 2010).
- Tillman, M.F. and Mizroch, S.A. 1982. Mark-recapture estimates of abundance for the western northern Pacific stock of Bryde's whales. Reports of the International Whaling Commission 32: 335-337.
- Van Waerebeek, K.V., Baker, A.N., Félix, F., Gedamke, J., Iñiguez, M., Sanino, G.P., Secchi, E., Sutaria, D. van Helden, A., Wang, Y. 2007. Vessel collisions with small cetaceans worldwide and with large whales in the southern hemisphere, an initial assessment. Latin American Journal of Aquatic Mammals 6: 43-69.
- Wade, P. R. and Gerrodette, T. 1993. Estimates of cetacean abundance and distribution in the eastern tropical Pacific. Reports of the International Whaling Commission 43: 477-493.
- Wang, J.Y., Yang, S.-C., Liao, H.-C. 2001. Records of melon-headed whales, *Peponocephala electra* (Gray 1846), from the waters of Taiwan. Bulletin of the National Museum of Natural Science 14: 85-91.
- Walker, E.P., Stoner, D., Shadle, A.R., Eaton Jr., T.H., Davis, W.B., Goodwin, G.G., Stager, K.E., Krutzsch, P.H., Green, M., Foster, C.A., Teeters, R., Rowan, W., Jacobs, D.L., Wilns, L.W. 1945. Journal of Mammalogy 6: 192-200.
- Watkins, W.A., Daher, M.A., Samuels, A., Gannon, D.P. 1997. Observations of *Peponocephala electra*, the melon-headed whale, in the southeastern Caribbean. Caribbean Journal of Science 33: 34-40.
- Wells, R.S. and Scott, M.D. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-recapture techniques. Reports of the International Whaling Commission Special Issue 12: 407-415.
- White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: 120–138.
- Whitehead, H. 2001. Analysis of animal movement using opportunistic individual identifications: Application to sperm whales. Ecology 82: 1417-1432.

Wilkes, C. 1845. Narrative of the United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842. Vol. 4. Lea and Blanchard, Philadelphia, PA.

Woodworth, P., Schorr, G.S., Baird, R.W., Webster, D.L., McSweeney, D.J., Hanson, M.B., Andrews, R.D., Polovina, J.J. *Submitted*. Eddies as offshore foraging grounds for melon-headed whales (*Peponocephala electra*).

Würsig, B. and Jefferson, T.A. 1990. Methods of photo-identification for small cetaceans. Reports of the International Whaling Commission. Special Issue 12: 42-43.

Chapter Two

Population Size and Structure of Melon-Headed Whales (*Peponocephala electra*) around the Main Hawaiian Islands: Evidence of Multiple Populations Based on Photographic Data

Introduction

Cetaceans are distributed worldwide, in every ocean of the world including coastal, oceanic, and even some riverine habitats. Some species occur over a broad range of habitats, such as humpback whales (*Megaptera novaeangliae*), found in both the Northern and Southern hemisphere, where they travel thousands of miles while migrating between cooler productive feeding grounds and warmer, but less productive, breeding grounds. Other species are restricted to small niches, such as the highly endangered vaquita (*Phocoena sinus*), whose habitat is limited to a small area in the northern part of the Gulf of California. Globally, more than 80 species of cetaceans are recognized (Reeves et al. 2002). Despite its isolation in the Pacific, more than 3,000 km from the continental United States, Hawaiian waters are home to at least 24 species of cetaceans, which includes 18 species of odontocetes and six species of mysticetes (Barlow 2006). Until recent years, most of the research conducted in these waters focused on only two species, humpback whales (e.g. Herman and Antinoja 1977) and the spinner dolphin (*Stenella longirostris*) (e.g. Norris et al. 1994). Lack of scientific information pertaining to the other species has fueled both an increase in dedicated research, and a general understanding of the need for continued research, with regards to Hawai‘i’s less studied species.

One such species that is receiving increasing attention, but is still poorly studied, is the melon-headed whale (*Peponocephala electra*), a smaller odontocete found in tropical and subtropical waters worldwide (Perryman et al. 1994). Melon-headed whales received unsolicited notoriety in 2004 when a group of 150 – 200 animals entered the shallow waters of Hanalei Bay,

Kaua‘i, coincident with mid-frequency sonar use during a naval training exercise (Southall et al. 2006). This event set off a flurry of debate as to whether sonar was truly to blame (e.g. Fromm et al. 2006, Mobley et al. 2007, Brownell et al. 2009), and in the process made transparent the lack of available accurate information on some of the basic biological parameters, including life history, range, and population size of this species. This lack of scientific information is due in part to the fact that melon-headed whales are often found in deep, offshore waters, making scientific study difficult.

Population information specific to melon-headed whales in Hawai‘i is limited to two abundance estimates. The first estimate comes from aerial surveys conducted between 1993 and 1998 aimed at estimating abundance of all marine mammal species within 46 km of the Main Hawaiian Islands (Mobley et al. 2000). Three sightings of melon-headed whales were reported, and two of the sightings were used in order to estimate an abundance of 154 with a coefficient of variation (CV) of 0.88 (Mobley et al. 2000). Several sources of negative bias were noted (Mobley et al. 2000), therefore abundance was likely underestimated. The second estimate comes from a line-transect ship survey of cetacean abundance in the waters of the Exclusive Economic Zone (EEZ) surrounding both the Northwest and Main Hawaiian Islands (Barlow 2006). During this survey there was only one sighting of melon-headed whales, and abundance in the Hawaiian EEZ was estimated at 2,950 (CV = 1.17) (Barlow 2006). As a result of the small number of sightings both estimates have a low degree of precision.

Photo-identification offers another means by which to estimate population size, and can be considerably more precise than abundance estimates generated from line transect surveys when there are high re-sighting rates (Hiby and Hammond 1989). In many delphinids, unique markings and notches along the trailing edge of the dorsal fin can be used to identify individual

animals (Hammond 1986, Wells and Scott 1990). When re-sighted, the encounter histories from individual animals can be used in mark-recapture analyses in order to estimate population size. In addition to mark-recapture analyses, re-sighting information can provide a wealth of additional knowledge. Frequent re-sightings suggest that the survey efforts are successful in identifying a high percentage of a given population, whereas a low re-sighting rate suggests that a large proportion of the population is still unknown (i.e. has not been photographed). Examination of photographic history of photo-identified individuals can also be used to assess movements, fidelity, residency, and associations. Association patterns can be used to assess population structure; in such association analyses, when dealing with a single population, all individuals would be ‘connected’ by association, and when dealing with more than one population, multiple groups of connected individuals would emerge. This study uses multi-year photographic data to assess site fidelity, population information, and to better estimate population size for melon-headed whales around the Main Hawaiian Islands.

Methods

Field Methods

Directed surveys for odontocete cetaceans took place around the Main Hawaiian Islands between 2000 and 2009 using small research vessels (generally under 9 m). Field work typically consisted of daily surveys based off one island for durations of two to six weeks. Although surveys were not systematic, they were also non-random in that they were designed to survey a broad area over a range of depths (Figure 2.1). Detailed field methods have previously been described by Baird et al. (2008a) and are therefore only summarized here. GPS locations were logged automatically every five minutes during transit. Two to five field observers scanned 360°,

and when a group was encountered, species information was collected including the sighting cue, Beaufort sea state, initial behavior, and direction of travel (Appendix 1). Photos were taken with film cameras through 2002 and with digital cameras from 2003 on, by one to four photographers. Every effort was made to photo-identify all individuals within a group with no regard for how well-marked an individual was. When possible, both left and right side photographs were taken, as well as multiple photographs of the same individuals. Depending on the priorities of a given survey, biopsy samples were sometimes collected for genetic analysis, and beginning in 2008, satellite tags were deployed on some individual melon-headed whales (see Schorr et al. 2009). At the end of each encounter, additional information was recorded, including the estimated group size (minimum, maximum, and best), behavior, direction of travel, group envelope, estimated percentage of the group observed, number of neonates and young of year, numbers of individuals with cookie cutter shark (*Isistius brasiliensis*) wounds, the presence of other species, the reason for leaving, and beginning November 2006, the presence of fishing vessels. The distance from shore and start depth were read directly off the GPS.

Photographs of melon-headed whales were taken at each sighting location and occurred off the islands of Hawai‘i, O‘ahu, and Kaua‘i/Ni‘ihau (Appendix 2). A number of pre-study photographs taken between 1986 and 2001 were made available courtesy of Dan McSweeney of the Wild Whale Research Foundation. Additional photographs collected between 2005 and 2010 were also made available by Southwest Fisheries Science Center (SWFSC), Pacific Islands Fisheries Science Center (PIFSC), and Michael Richlen of the University of Hawai‘i, Mānoa. While the full photographic data from all years and all sources was used in creating the catalog and determining re-sighting information, all other results, such as depth, distance from shore, and

group size, were compiled using only the comprehensive data collected from the directed surveys through 2009.

Photo-Identification

The photo-identification catalog was compiled following the same protocol used in other Hawaiian odontocete catalogs (e.g. Baird et al. 2008a, 2008b, Baird et al. 2009, McSweeney et al. 2009). Photo sorting and matching was performed in ACDSee Pro v. 2.0 and 2.5, without the use of any additional photo matching software. Photographs were first sorted by encounter so that all animals identified within an encounter were given a temporary identification number and a corresponding electronic file folder. Individuals were sorted primarily through the use of unique notches along the trailing or leading edge of the dorsal fin, as well as other features such as dorsal fin shape, pigmentation, or other scarring. When possible, individuals that had no unique markings or notches were also sorted by individual using fin shape and temporary markings such as rakes or cookie cutter shark bite wounds.

This project continued the work of an in-progress catalog that contained 533 unique identifications (Huggins et al. 2005). Therefore, each temporary identification was compared to every individual in this catalog. If the individual was not found in the catalog, it was assigned a new catalog identification in the form of “HIPe####.” The best photograph of each individual was assigned a photo quality rating, ranging from 1 – 4 where 1 = poor, 2 = fair, 3 = good, and 4 = excellent quality (Figure 2.2). This rating was based on a number of photo qualities, such as focus of the image, distance, and the angle of the dorsal fin relative to the frame. Use of the term “well-photographed” throughout the chapter will refer to individuals with photo quality ratings of 3 or 4. Notches along the trailing edge of the dorsal fin were noted for each individual, as was

the presence of leading edge dents (LED), leading edge notches (LEN), top notches (TN), or peduncle notches (PN). Identifications were then assigned a distinctiveness rating, also ranging from 1 – 4 where 1 = non-distinctive, 2 = slightly distinctive, 3 = distinctive, and 4 = very distinctive (Figure 2.3). Very distinctive dorsal fins typically had multiple notches along the trailing edge and/or disfigurements along the top or leading edge of the dorsal fin. Distinctive dorsal fins had similar types of markings but to a lesser extent. Slightly distinctive dorsal fins had few notches along the trailing edge. Non-distinctive dorsal fins usually had no notches along the trailing or leading edge; while these individuals could sometimes be sorted within a single encounter based on fin shape and temporary markings, they could not reliably be matched between encounters, and therefore were not included in the catalog. Because mark-recapture analyses were done using only those individuals rated distinctive or very distinctive, it was necessary to determine the ratio of individuals that were non-distinctive and slightly distinctive to correct abundance estimates to account for all individuals. These analyses were restricted to encounters with 20 or more individuals to reduce variance due to small sample sizes. Photo quality and distinctiveness ratings, along with date, encounter, island, number of notches, additional scars or markings, associations, and additional comments were recorded in an Excel worksheet.

Each dorsal fin match was confirmed by at least two experienced matchers (someone with more than two years experience with cetacean photo-identification matching). Over time, it is possible for dorsal fin markings to change, either with the addition of new nicks and/or notches or the smoothing out and eventual loss of nicks and/or notches. Mark changes were documented in order to estimate the rate of mark change. In order to determine a “missed-match

rate,” a number of cataloged individuals were taken through the full catalog again by an additional experienced matcher.

Additional information was obtained from the photographs, including an assessment of dorsal fin and bodily injuries, as well as the presence of neonatal and larger calves. Scarring or disfigurement due to line or rope entanglement was determined based on the resulting injuries, usually in the form of grooved indentations from having a line wrapped around the dorsal fin. Injuries from being shot at were categorized based on circular openings going all or part of the way through the dorsal fin. Predatory or conspecific injuries were classified from apparent bites or extensive raking. Neonatal calves were recognized by fetal folds along the body. Because calves were most often not-distinctive (with the exception of individuals with injuries from cookie cutter shark bites), the number of calves in an encounter was determined by identifying the adult in which they were associating with (i.e. swimming alongside or within one body length of). To determine the proportion of neonates per month, the total number of neonates seen by month was divided by the sum of the group size by month.

Mark-Recapture Analysis

The encounter histories from all fully sorted encounters, using only distinctive or very distinctive individuals with a photo quality rating of good or excellent, were used to estimate abundance with MARK v. 6.0 (White and Burnham 1999). Based on the multi-year time frame of the study, use of an open population model was more appropriate than a closed model; however, a trade-off exists when choosing an open population model over a closed one. While the assumptions of a closed population model clearly could not be met (i.e. that the population was closed to births, deaths, immigrations, and emigrations), violations of model assumptions are

also possible for open population modeling. These assumptions, modified from Seber (1982), and sometimes referred to as the Cormack-Jolly-Seber (CJS) assumptions, are:

1. Every animal in the population at time (i) has the same probability of recapture (p_i) (equal catchability).
2. Every marked animal in the population immediately following time (i) has the same probability of surviving to time ($i + 1$) (equal survivorship).
3. Marks are not lost or missed.
4. Sampling is instantaneous.

POPAN (Schwarz and Arnason 1996), a Jolly-Seber formulation within MARK, can directly estimate abundance (N), and was therefore the preferred formulation for analyses. Encounter histories for Jolly-Seber-type models consist of a series of 1's and 0's, each indicative of either the presence (1) or absence (0) of a given individual at each sighting occasion (Figure 2.4). For example, an encounter history of (100010) translates to six encounter occasions; after an initial sighting, the individual was not seen in the three following occasions, was seen on the fifth occasion, but not seen on the last occasion. Encounter occasions may be looked at in their entirety, or they may be condensed into bins, such as by month or year. POPAN uses a number of parameters to estimate N , the super-population, or the number of individuals using the study area for the duration of the study period. Other parameters used in the POPAN model are ϕ , the apparent survival; p , the probability of capture; and b , the probability that an animal from the super-population would enter into the population between occasions (referred to as *PENT*, or probability of entrance, in MARK). When building models in MARK, each of these parameters (ϕ , p , *PENT*) can also be denoted with the subscripts “ t ” or “.” which corresponds to the parameters being either time-dependent (t) or constant (.) (after Lebreton et al. 1992). The fully time-dependent model, or global model, is therefore denoted as: $\phi(t)$ $p(t)$ *pent(t)*.

Data subsets were assembled in order to represent a variety of biological possibilities and within each subset a number of different models were run using a combination of the specified restraints on each parameter. The best model within each subset was chosen using Akaike's Information Criterion (AIC). The AIC is calculated as:

$$AIC = -2\ln(\mathcal{L}) + 2K \quad (2.1)$$

where \mathcal{L} is the model likelihood and K is the number of parameters in the model. The better the model fits the data, the more likely the model is, and therefore the first part of the equation, $(-2\ln(\mathcal{L}))$, will have a small value. The fewer parameters that are used, the more precise the model will be, and therefore the second part of the equation, $(2K)$, will also have a small value. As the number of parameters increase, so does the AIC value. Similarly, models that do not fit the data well will also be charged with an enlarged AIC value. Essentially, models with a low AIC value are considered to be the “best” models – these models best fit the data and have the fewest number of parameters. That being said, AIC values deal with numbers, not biology. It is therefore important to determine that the model not only has a low AIC value, but also makes sound biological sense. The Akaike Information Criterion may not function effectively if there are too many parameters in relation to the sample size; therefore MARK reports a corrected AIC value, referred to as AICc, calculated as:

$$AICc = AIC + \frac{2P(P + 1)}{(n - P - 1)} \quad (2.2)$$

where P is the number of estimated parameters, and n is the number of observations.

Prior to building supplementary models in MARK, it is first important to ensure that the global model adequately fits the given data. Using the POPAN formulation, goodness of fit (GOF) can be tested using program RELEASE (Burnham et al. 1987). Goodness of fit compares the observed versus the expected sighting history for each individual at each sampling occasion.

Lack of fit generally arises when a model's assumptions have been violated, and the two assumptions most likely to be violated are that all animals have the same probability of recapture and all animals have the same probability of survival. Program RELEASE provides a series of tests; the three most widely used are TEST 2, TEST 3, and TEST 2 + TEST 3. In general, TEST 2 examines the assumptions of equal catchability, whereas TEST 3 examines the assumptions of equal survivorship. TEST 2 + TEST 3 results provide information on overdispersion in the data. If lack of fit is suspected based on the results of the GOF tests, corrections can be made by calculating a variance inflation factor, \hat{c} (Lebreton et al. 1992). This parameter can then be used to adjust AICc values to QAICc (Quasi-AICc) values, calculated as:

$$\text{QAICc} = \frac{-2\ln(\mathcal{L})}{\hat{c}} + 2K + \frac{2K(K+1)}{n-K-1} \quad (2.3)$$

The POPAN open population formulation in MARK was used in order to estimate the super-population of melon-headed whales around the Main Hawaiian Islands during the study period. Population structure was assessed based on associations of individuals between groups, and Netdraw (Borgatti 2002) was used to illustrate association patterns. Re-sighting information was used in order to evaluate site fidelity, and those re-sightings from individuals seen off a different island from where they were initially photographed were used to determine inter-island movements. The analysis of the pre-study photographs was used in order to determine the long-term residency of melon-headed whales in Hawai‘i.

Results

Sighting and Encounter Summary

Between February 2000 and December 2009, a total of 56,132 km of trackline was covered during 504 days on the water (3,650 hours on effort). The majority of fieldwork occurred off the leeward side of the island of Hawai‘i, where depth, weather, and sea conditions make survey work favorable. Although attempts were made to distribute survey effort as widely as possible during each field project, during winter months (November through mid-April) survey areas were often more restricted, with less coverage in areas that were more exposed to trade winds (e.g., north of Keahole Point on the island of Hawai‘i). In total, there were 1,291 sightings of 18 species of odontocetes , and melon-headed whales were the 8th most frequently encountered species, representing only 2.6% of all sightings, and occurring on average once every 14 days on the water.

During this directed survey effort there were 36 encounters with melon-headed whales that occurred on 31 different days around the Main Hawaiian Islands. Thirty one sightings were cued by the observation of an animal at the surface (either a splash, blow, or fin), four were cued from radio calls, and one was cued from another vessel. Four encounters occurred off the islands of Kaua‘i and Ni‘ihau, one encounter occurred off the island of O‘ahu, and the remaining 31 encounters occurred off the island of Hawai‘i (Figure 2.5). Despite 8,178 km (682 hours) of effort off the 4-island area (Maui, Lana‘i, Moloka‘i, and Kaho‘olawe) and sightings of 107 odontocete groups, there were no sightings of melon-headed whales in this area. Encounter duration from directed efforts ranged from 9 min – 4 hrs, 41 min (median = 1 h, 19 min) and initial Beaufort sea state for sightings ranged from 0 – 3 (median = 1).

Twenty six encounters (72.2%) either began or ended with the group traveling. Most often travel was slow, and on only two occasions was it fast (one of the two occasions was when killer whales were also present). In 20 encounters (55.5%), start and/or end behavior involved milling, logging, resting, or socializing (with behaviors being non-mutually exclusive). Fishing vessels were seen in three of 13 (23.1%) encounters since 2008 and anecdotally recorded on one occasion prior. At least four fishing boats were seen trolling through groups of animals.

Group size ranged from a single animal to a best estimate of 800 individuals (median = 275). The one encounter with a single individual involved an animal that was in poor body condition, both in terms of probable emaciation and skin condition (Figure 2.7). The animal was heavily marked with open cookie cutter shark wounds (at least seven were visible dorsally) and also had areas of discoloration covering its body, indicative of poor survival likelihood. The next two smallest encounters (4 and 17 individuals) were both followed shortly thereafter by encounters with larger groups of animals (275 and 350, respectively), suggesting the animals may have branched off from a main group. Distance from shore ranged from 3.1 – 43 km (median = 13.1 km).

Between 2005 and 2009, photographs from seven additional opportunistic encounters off the island of Hawai‘i on six additional days, and four encounters off the island of O‘ahu on four different days were also made available. Survey efforts, and therefore sighting locations, occurred off the leeward side of each island, with the exception of Kaua‘i/Ni‘ihau where favorable sea conditions allowed for efforts that circumnavigated the entire island. Beaufort sea state for sightings ranged from 0 – 3 (median = 1), and at least one encounter occurred in each month of the year, providing year-round sighting information. A total of 31,411 photographs from 40 encounters between 2002 and 2008 were available, as well as 9,380 photographs from

seven encounters in 2009, and an additional 2,062 pre-study photographs taken from the island of Hawai‘i between 1986 and 2001 (Appendix 2). Photos taken in 2009 (which included the four encounters off O‘ahu) were examined only briefly to determine whether the photographed groups of melon-headed whales contained matches to individuals already in the catalog and if so to what other encounters.

Evidence of Multiple Populations – Social Network Analysis and Sighting Locations

A social network diagram including all well-photographed, distinctive individuals (Figure 2.8) shows that most ($820/1,046 \approx 78.4\%$) individuals were linked by association in a single cluster (referred hereafter as the “Main Hawaiian Islands population”). One hundred and eighty ($\approx 17.3\%$) individuals were linked in a second large cluster (referred hereafter as the “Hawai‘i resident population”), and there were three small clusters that included the remaining 45 ($\approx 4.3\%$) individuals. These three small clusters included one encounter off the island of O‘ahu (with 18 individuals) and two encounters off the island of Hawai‘i (with three and 25 individuals).

To assess whether associations between these clusters may actually occur but were missed because of the restriction of analyses to only the well-photographed distinctive individuals, a social network diagram was produced loosening the restrictions to also include fair photo quality images and slightly distinctive individuals. When doing so, one of the small clusters (from an encounter off the island of O‘ahu) linked to the main cluster, and slightly increases the percentage of individuals who link to the Main Hawaiian Islands population ($1,316/1,622 \approx 81.1\%$) (Figure 2.9). The percentage of animals in the second to largest cluster, the Hawai‘i residents, decreased slightly ($250/1622 \approx 15.4\%$) as did the remaining two smallest

clusters ($57/1,622 \approx 3.5\%$). Individuals from the two smallest clusters were seen on only one occasion; therefore, it is hard to infer whether or not they would be linked to the main cluster given additional sightings. The smallest cluster contained only five individuals (three when restricting to well-photographed, distinctive IDs), and since approximately one out of every three distinctive well-photographed animals were re-sighted, the lack of re-sights from this smallest cluster is not surprising. From the second smallest cluster, there were 52 individuals (26 when restricting to well-photographed, distinctive IDs) that were photographed off the island of Hawai‘i; given the re-sighting rate, it is more surprising that none of these individuals would link to the main cluster. Additional sighting history is needed for these individuals to determine if they would link to the main cluster or not.

The second to largest cluster contained 180 well-photographed, distinctive individuals from six encounters (Figure 2.10). Sixty-four of these individuals (35.6%) were seen on two or more occasions. Re-sighting frequency varied by island area (Table 2.1), although even the most conservative assessment indicates that at least one out of every six individuals was seen on more than one occasion. Therefore a minimum of 30 re-sightings between the two large social networks would be expected if they were all from a single population.

Sighting locations for all encounters were off the leeward side of the islands being surveyed, with the exception of one encounter off Kaua‘i, that occurred to the north of the island (Figure 2.11). When mapping sighting locations of melon-headed whales around the Main Hawaiian Islands, the locations of the nine encounters from dedicated surveys with the resident group are clustered, occurring in the waters off the northwestern region of the island of Hawai‘i (Figure 2.15, 2.16). Of the other 21 encounters from the dedicated surveys that occurred off the island of Hawai‘i, 20 of the sightings took place south of the region in which the resident

population was found. The one encounter from dedicated surveys with the group of animals that currently do not link by association to either the Hawai‘i resident or the Main Hawaiian Islands population occurred off the island of Hawai‘i and was the westernmost encounter for the species off this island. Such data strongly supports the idea that at least two populations of melon-headed whales are using adjacent, and sometimes overlapping, habitats.

The restricted range of the Hawai‘i resident population is further supported when looking at the number of sightings per unit effort. In total, 523 hours of dedicated effort occurred north of Keahole Point, Hawai‘i (Figure 2.14). In this area, there were 11 sightings of the Hawai‘i resident population, representing on average one sighting for every 48 hours of effort. Only one sighting of the Main Hawaiian Islands population occurred north of this same area, and one sighting with the group of animals that may or may not be part of the Main Hawaiian Islands population. When including all surveyed areas, encounters with the Main Hawaiian Islands population occurred on average once every 140 hours of effort.

Sightings for all encounters occurred at depths ranging from 285 – 4,772 m (median = 1,400 m, n = 35) (Figure 2.15) and between 3.1 and 43.0 km from shore (median = 9.9 km). Encounters with the Hawai‘i residents occurred in substantially shallower waters, ranging from 285 – 895 m (median = 381 m, n = 9). When excluding these residents, overall depth of melon-headed whale sightings increased for all areas (median = 1,844 m, n = 26) and for those encounters just off the island of Hawai‘i (median = 1,860 m, n = 21). The depth of encounters with residents was significantly shallower than for the Main Hawaiian Islands population (Mann-Whitney *U* test, $P < 0.0001$). Distance from shore was not considerably different for the residents (median = 9.4 km) compared to all other individuals off the island of Hawai‘i (median

– 10.1 km). Survey efforts, and therefore distance from shore and depths, varied off each island region, and as a result, distance from shore and start depth are not comparable between islands.

Twelve out of the 36 encounters (33.3%) were mixed encounters with one or more additional species. While both the Main Hawaiian Islands population and the Hawai‘i resident population were seen associating with other species, the residents were only seen associating with humpback whales ($n = 2$), whereas groups from the Main Hawaiian Islands population were seen with five species, including rough-toothed dolphins ($n = 6$), short-finned pilot whales ($n = 3$) (Figure 2.6), pantropical spotted dolphins ($n = 1$), killer whales ($n = 1$), and Fraser’s dolphins ($n = 1$).

Photo-Identification

Usable photographs were collected in all but one encounter. From the photographs collected between 2002 and 2008, 28 encounters were fully processed (i.e., sorted and matched to the catalog in their entirety). Of the remaining 12 encounters, nine were fully sorted and three were partially sorted. These 12 partially sorted encounters from 2002 – 2008, along with the seven encounters in 2009, were all examined at some level to ensure that there were individuals within the encounter that matched back to the catalog. Matches to either the main cluster or the resident cluster were found in all of the partially processed encounters.

From the number of notches on the trailing edge of the dorsal fin, non-distinctive individuals had 0 – 1 notches (median = 0), slightly distinctive individuals had 0 – 9 notches (median = 2.5), distinctive individuals had 0 – 15 notches (median = 5), and very distinctive individuals had 0 – 12 notches (median = 5). The one very distinctive individual with no notches had an extremely unique fin-shape, which allowed classification into this category. While the

median number of notches for both distinctive and very distinctive individuals was the same, notches for the very distinctive individuals tended to be larger or more prominent than those of the distinctive animals. Thirty-seven percent of slightly distinctive individuals, 63% of distinctive individuals, and 90% of very distinctive individuals had at least one leading edge dent, leading edge notch, top notch, or peduncle notch.

The proportion of marked to unmarked individuals varied by encounter. By encounter, the percentage of distinctive or very distinctive individuals ranged from 53.4 – 64.0% (median = 61.8%, CV = 0.06; n = 6). The percentage of distinctive and very distinctive animals in the Hawai‘i resident population ranged from 53.4 – 62.0 (median = 57.7, CV = 0.11; n = 2), and was only slightly less than the percent distinctive for the Main Hawaiian Islands population which ranged from 59.5 – 64.0 (median = 61.9, CV = 0.03; n = 4). Because of the few number of encounters used to determine the percentage distinctive for the resident population, the overall percentage distinctive was used to correct population estimates for both the Hawai‘i resident and Main Hawaiian Islands populations. In order to compare the distinctiveness results for the Hawai‘i populations with melon-headed whales elsewhere, the proportion distinct was recalculated to also include individuals considered to be slightly distinctive. This calculation more closely resembles methods used by Kiszka et al. (2008) where melon-headed whales around the Mozambique Channel Island of Mayotte were categorized into only two categories – those that had any notches and those that did not. Including the slightly distinctive individuals produced a median “identifiable” percentage of 84.9% for melon-headed whales in Hawai‘i.

While 1,640 unique individuals were included in the catalog, 1,046 of these were distinctive or very distinctive with a photo quality rating of good or excellent. These 1,046 individuals were based on 1,356 identifications across all fully processed encounters. Ignoring

between-area re-sightings, off Hawai‘i there were 712 distinctive individuals, off Kaua‘i/Ni‘ihau there were 316, and off O‘ahu there were 18 (Table 2.1). From these fully-sorted encounters, there were 310 re-sightings of 250 individuals, representing an overall re-sighting rate of 23.9% (Table 2.1). From both the fully and partially sorted encounters there were 716 individuals seen only one time and 328 individuals seen on two or more occasions (Figure 2.16). The maximum number of times an individual was seen was eight. The number of photographs taken of each individual during an encounter varied (range 1 – 164, median = 4).

While the total number of identifications can be used as a bare minimum population estimate, discovery curves shows that the cumulative number of melon-headed whale identifications never reached an asymptote, indicating that the number of individuals identified is not a true representation of the total number of individuals in the population (Figure 2.17). However, based on the multi-year time frame of this study, new distinctive individuals would continue to be recruited to the population based on individuals acquiring marks (approximately 20 annually to the Hawai‘i resident population, and 160 annually to the Main Hawaiian Islands population); therefore, the line would not be expected to asymptote entirely. The slope of the line for the residents is less steep than both the slope of the Main Hawaiian Islands population and the combined populations, suggesting that the number of resident identifications is closer to the true population in comparison to the other two discovery curves.

From all fully sorted encounters, including only the distinctive or very distinctive individuals with a photo quality rating of good or excellent, the percentage of individual melon-headed whales within-groups that were documented on more than one occasion (either before or after) ranged from 0 – 92.9% (median = 34.7%). Excluding those encounters with fewer than ten identifications, the median number of individuals within-groups seen on more than one occasion

was 41.0%. From encounters with just the Hawai‘i resident population, the median increased to 62.0%, and excluding the residents, the median percentage of individuals documented on more than one occasion decreased to 36.9%. Although the percentage of individuals re-sighted off the Kaua‘i / Ni‘ihau island regions is higher than for Hawai‘i, this presumably reflects a positive bias, as all re-sightings occurred over the course of three encounters in a six day period (and likely from the same group of individuals). The number of re-sightings off Hawai‘i shows a high number of between-year re-sightings, reflective of the increased surveys efforts off this island region. With only one directed survey effort off O‘ahu, the number of identifications is very low in comparison to other island regions. Although the restriction on this analysis prevented any re-sightings to be included, brief examination of four encounters from October 2009 off the island of O‘ahu show that there are in fact several matches from each encounter to the Main Hawaiian Islands population. Re-sightings from these encounters include individuals who were last seen in an April 2008 encounter off Hawai‘i, a June 2008 encounter off Kaua‘i, and an encounter four years previously off Hawai‘i.

The Hawai‘i residents showed the highest percentage of individuals re-sighted (35.6%), with 72.3% of re-sightings occurring between-years. When including encounters that were partially sorted, the proportion of resident individuals that were re-sighted jumps to 57.9%. Excluding the Hawai‘i residents, the proportion of individuals re-sighted off the island of Hawai‘i was only 16.9% (23.4% when including the partially sorted encounters), and is indicative of a large population.

While the focal period of this study was between 2000 and 2009, re-sightings of individual melon-headed whales dated as far back as the first year photos were available, 1986, suggesting long-term residency to the Main Hawaiian Islands. A total of eight re-sightings of

pre-study animals were documented thus far, two from the Main Hawaiian Islands population, and six from the resident population. The current longest re-sighting from an individual of the Main Hawaiian Islands population was 13 years from an individual seen in 1995, 2004, and 2008. The longest and most comprehensive re-sighting overall spans more than 22 years and comes from a very distinctive individual, HIPe1579, a member of the resident population who was seen in 1986, 1996, 2005, 2006, and 2008 (Figure 2.18). There are also at least two more re-sightings from this April 1986 encounter that match to individuals most recently sighted in 2008. The length of time between the initial and final sighting of an animal therefore ranged from 1 – 8,277 days (22.6 years) (median = 124 days) when including animals seen prior to 2002. For individuals from the resident population, the time span was the same; however, the median number of days between the first and last sighting of an animal was 990 (2.7 years) (both when including and excluding the pre-study re-sightings). For individuals of the Main Hawaiian Islands population, the time between the initial and final sighting of an animal ranged from 1 – 4,792 days (13.1 years) (median = 5 days). The median value shows negative bias based on the high number of re-sightings that occurred during the same trip (i.e. over the course of several days or weeks). When these within-trip sightings were excluded, the median value of time between the first and last sighting of an animal increased to 691 days (1.9 years) (median = 664 days (1.6 years) when excluding pre-study re-sightings).

From good quality photos of all distinctive individuals from both populations, there were 214 between-year re-sightings and 265 within-year re-sightings. The number of within-year re-sightings is somewhat artificially inflated due to seeing the same individuals on more than one occasion during the same trip. Therefore, the number of within-year re-sightings was recalculated to only include individuals seen on different trips (minimum time between different

trip re-sightings = 66 days), resulting in 66 within-year re-sightings. Assessing only the re-sightings of individuals comprising the Main Hawaiian Islands population, and when within-trip re-sightings were excluded, there were 29 between-island (area) re-sightings of 29 individuals and 100 within-island (area) re-sightings of 73 individuals. Individuals comprising the Hawai‘i resident population were more often re-sighted between years (113 re-sightings) than within year (72 re-sightings). Within-year re-sights for the resident population drops to 28 when excluding the within-trip re-sightings.

At least 66 individuals were documented in close association with the same animal(s) on more than one occasion. Associations were defined as individuals swimming alongside one another or within one body length of each other (Figure 2.19). Although mother-calf pairs would qualify in terms of such associations, lack of distinctiveness on the part of the calves prevented these pairs from being included in this minimum estimate. Individual associations were not recorded until approximately half way through the catalog; therefore, this is most certainly an underestimation of the true number of such associations. The maximum number of times two or more animals were seen together was three, and the maximum length of time between such associations was ten years.

Of the 330 well-photographed, distinctive individuals who were re-sighted, 36 incurred changes to either the number or shape of a dorsal fin notch, representing approximately 10.9% of all well-photographed, distinctive re-sightings (Figure 2.20). This included four individuals who underwent multiple independent mark changes. Of the 36 individuals, 23 were from the Hawai‘i resident population, and 13 were from the Main Hawaiian Islands population. Two individuals from the Main Hawaiian Islands population who underwent mark changes due to tagging attempts were excluded from these calculations since the changes were considered to occur

artificially. Taking into consideration that multiple mark changes between re-sightings could have occurred on either a single or multiple occasions, of 60 documented mark changes, the minimum number of mark change events was 40. Therefore, to calculate how often mark changes occurred in melon-headed whales, the time between the first and last sighting for all individuals seen on more than one occasion was summed (201,524 days = 552.1 years) and divided by the minimum (40) and maximum (60) number of mark changes that occurred, to produce a value of one mark change every 9.2 – 13.8 years (Table 2.2). However, based on the differences in the number and percent of individuals with mark changes between the two populations, the occurrence of mark changes was re-calculated to assess the two populations independently. For the resident population, a mark change is estimated to occur every 6.7 – 10.3 years, and once every 15.2- 21.0 years for the Main Hawaiian Islands population.

In order to assess the rate of missed matches, a number of cataloged individuals were systematically taken through the catalog a second time by another experienced matcher. Of 76 individuals who were taken back through the catalog, six were found to have already been catalog identifications (a false positive error). This produced a missed-match rate of ~8%, or a successful matching rate of ~92%, similar to rates estimated from other photo-identification studies (e.g. Calambokidis et al. 2008). Of the six individuals found to be repeated in the catalog, five were rated distinctive, and one was rated very distinctive; two had photo quality ratings of fair, and the remaining four had photo quality ratings of good. It does not, therefore, seem that any specific quality accounted for the occurrence of missed matches. Based on the quality rating, had these missed matches not been identified, four (~5%) of these missed matches may have been included in analyses. Such inclusions will cause a positive bias to population estimates by increasing the number of total identifications as well as decreasing the total number

of re-sightings. Throughout the matching process a number of additional missed matches were identified, both from the initial catalog ($n = 5$) as well as the in-progress catalog ($n = 9$). Left/right photographs of two identifications from the initial catalog were also discovered to be four different animals, rather than the two in which they had been assigned (a false negative error).

Mark-Recapture Estimation

Mark-recapture analyses were run with a variety of data combinations. In total, there were 1,046 well-photographed, distinctive individuals from 25 fully-sorted encounters over the course of 22 different days (spanning six years) that were available for use in the analyses. For the initial mark-recapture analysis, the full encounter history for all individual melon-headed whales was entered into MARK v 6.0 (White and Burnham 1999). A program RELEASE (Burnham et al. 1987) goodness of fit test was performed on the fully time-dependent $(\phi(t)p(t)pent(t))$ model. Recall in POPAN, ϕ = apparent survival, p = probability of capture, and $pent$ = probability of entry into the group, with the subscripts (t) referring to time dependency and (.) = constant. Results of TEST 2 + TEST 3 indicated that goodness of fit, and therefore model structure, was unsatisfactory ($\hat{c} = 6.99$). Lebreton et al. (1992) recommend that \hat{c} not exceed ≈ 3 . This result was somewhat anticipated, based on the significant variation in the number of identifications per encounter. The data was therefore rearranged and grouped into annual histories for the years 2003, 2004, 2005, 2006, and 2008. Data from 2007 was excluded based on the small number of identifications that year (10). Restricting the data in this way and later incorporating the percentage of less distinctive individuals can also help to overcome

sensitivity to heterogeneity (Hammond 1986). A program RELEASE (Burnham et al. 1987) goodness of fit test was performed on the annual fully time-dependent model. Although there was insufficient data to carry out TEST 3, TEST 2 was successful and from this goodness of fit was considered satisfactory; therefore, no variance inflation factor was applied. The top two models (those that contained any value for model likelihood) were $\phi(t)p(.)pent(t)$ and $\phi(t)p(.)pent(t)$ (Table 2.3). In other words, the top models both held survival and probability of entry into the group to be time-dependent, and probability of capture to be either time-dependent or constant. Both of these models had very similar AICc values ($\Delta\text{AICc} = 0.59$) so a case can be made to select either model. Burnham and Anderson (1998) note that models differing by less than two units from the model with the minimum AICc value (i.e. ΔAICc) also provide good descriptions of the data. The model that held probability of capture to be constant produced an estimate of 4,320 (CV = 0.08) and the model that held it to be time-dependent produced an estimate of 3,961 (CV = 0.19). Based on the similar AICc values and model likelihood information for these two top models, a derived model averaging was performed to produce an estimate of 4,166 (CV = 0.14). POPAN produces a “super-population” estimate, so this refers to the total number of animals using the focal area throughout the duration of the study. Also recall that the estimated percentage of melon-headed whales that are distinctive in Hawai‘i is 61.8% (CV = 0.06); therefore, these population estimates need to be adjusted in order to account for the non-distinctive individuals. This can be done by simply dividing the \hat{N} population estimates by the percentage distinctive:

$$N = \frac{\hat{N}}{\text{Percentage Distinctive}} \quad (2.4)$$

The CVs can be combined by taking the square root of the sum of the squared CV values:

$$CV_{combined} = \sqrt{(Distinctiveness\ CV^2 + \widehat{N}\ CV^2)} \quad (2.5)$$

Thus the corrected population estimate for the model averaged result, taking into account the proportion of unmarked individuals, is 6,741 (CV = 0.14; 95% CI = 4,858 – 8,628).

However, based on the evidence of two populations, the Hawai‘i residents and the Main Hawaiian Island population, separate mark-recapture estimates are more appropriate. For the residents, sufficient data existed to obtain results from program RELEASE’s TEST 2, TEST 3, and TEST 2 + TEST 3, and results supported goodness of fit as indicated by $\hat{\chi}$ values (Table 2.4). The top models both held probability of capture and probability of entry into the group to be time-dependent, and apparent survival to be either time-dependent or constant ($\phi(\cdot)p(t)pent(t)$, $\phi(t)p(t)pent(t)$) (Table 2.3). Both of these models had similar AICc values ($\Delta AICc = 1.91$) so again, a case can be made to select either model. The model that held apparent survival to be constant produced a corrected estimate (taking into account the proportion of unmarked individuals in the population) of 448 (CV = 0.10), and the model that held it to be time-dependent produced a corrected estimate of 443 (CV = 0.10). Based on the similar AICc values and model likelihood information for these two top models, a derived model averaging was performed and resulted in an adjusted weighted population estimate of 447 (CV = 0.12; 95% CI = 375 – 519).

Finally, a mark-recapture analysis was run excluding the encounter history of the Hawai‘i resident population from the full encounter history of the other 866 individuals. Attempting to assemble these encounters into a variety of groupings, such as annual, or semi-annual, excluded a large number of sighting histories, and therefore there was not enough information to establish model validity based on the limited results from program RELEASE. Based on these findings,

the full encounter history was used to estimate the population of individuals comprising the Main Hawaiian Islands population. A program RELEASE goodness of fit test was once again performed on the fully time-dependent model. The results of TEST 2 and TEST 2 + TEST 3 indicated that there were violations of certain model assumptions, and therefore a variance inflation factor of $\hat{c} = 2.53$ was applied (Table 2.4). The best model was the fully time-dependent model, which produced a corrected population estimate of 5,794 (CV = 0.20; 95% CI = 4,337 – 7,254) (Table 2.3).

Additional Photographic Findings – Dorsal Fin and Bodily Injuries

A number of different bodily injuries were detected on the 1,646 individual melon-headed whales included in the catalog. One of the most common dorsal injuries documented were injuries suggestive of line entanglements (Figure 2.21). While no animal was documented with line or rope around any part of its body, line entanglements are usually evident as grooved depressions from where the line cut through the cartilaginous dorsal fin, or in some cases, on other parts of the animal's body (Figure 2.22). At least 50 individuals (~3%) showed some indication of line scarring, which included 39 individuals from the Main Hawaiian Islands population and 11 individuals from the resident population.

At least five melon-headed whales, four from the Main Hawaiian Islands population, and one from the Hawai‘i resident population, showed dorsal fin injuries that may suggest the animals were targets of shooting (Figure 2.23). Some of these injuries left circular openings in the dorsal fins, whereas others showed circular depressions on one side (presumably where the bullet entered), and circular scarring or pigmentation on the other side. These injuries were not

due to either biopsy darting or satellite tagging attempts (photos of all tagged individuals or individuals that were biopsy darted in the dorsal fin were checked to confirm).

Probable injury due to a propeller strike was identified on one melon-headed whale in from the Main Hawaiian Islands population based on linear marks found across the back and dorsal region (Figure 2.24). These injuries are not consistent with the more closely spaced rake marks that were documented on many individual melon-headed whales.

Finally, a number of additional noteworthy injuries were documented that may have been predator-related, or caused by other unknown sources (Figure 2.25). With the exception of the first individual, HIPe1215, who was seen once the day after its initial sighting, none of these animals were re-sighted. This could simply be due to chance, the animals may not have survived (whether due directly to the injuries or other causes), or the severity of the injuries may have changed the appearance of the dorsal fin so much that the animal was not correctly identified at future re-sightings.

Additional Photographic Findings – Mother-Calf Pairs

A number of mother-calf pairs were documented throughout the duration of this study. Neonatal calves were defined as those individuals with fetal folds (Figure 2.26), and occasionally their dorsal fins were still folded following birth. Neonates were seen in nine months of the year (all months except May, August, and December), although there were no directed surveys in August, and only a small number of photos available from May (Appendix 2). The proportion of neonates per month was highest in March ($n = 2.12$), April ($n = 1.22$), and June ($n = 0.91$). The mean number of photos per individual in these three months ranged from $3.05 - 6.63$ (median =

6.2). While there was no documentation of neonates in the month of May, this month had the fewest number of available photographs from dedicated surveys, the fewest number of individuals, and the smallest mean number of photos per individual ($n = 0.61$); therefore, further encounters and photographs would likely show the presence of neonates in May. The proportion of neonates per month was low in other months; January = 0.06, February = 0.18, July = 0.39, September = 0.19, October = 0.19, November = 0.13, and December = 0.0. The mean number of photos per individual in these months ranged from 1.28 – 4.29 (median = 2.02), and should therefore have been adequate to determine the presence of neonates. Larger calves, defined as young-of-year, were seen in all months except August, although the lack of directed surveys in this month, combined with a small number of photographs suggest that lack of effort, rather than the absence of calves, is causing this void. These findings suggest that birthing takes place year-round, although likely occurs most frequently from March through June.

A female, HIPe0657, was the individual seen most frequently (eight), and she was often seen with a calf. In February 2005, this individual was first photographed alone; in March 2006 she was seen with a small calf (although larger than a neonate). She was seen two times in December 2008; the first sighting she was photographed with a group that contained several smaller, clean-finned individuals (although not neonates or young-of-the-year). On the second sighting occasion in 2008, five days later, she was photographed alone. In October and December 2009, she was seen with what appeared to be a large calf (Figure 2.27). Mother-calf pairs were often seen with other mother-calf pairs, suggesting that these females may associate closely with one another.

Discussion

Despite the presence of melon-headed whales in tropical and subtropical waters worldwide, very little dedicated research has been carried out on this species. Few estimates of abundance exist, and those in Hawai‘i have high associated uncertainty (i.e., Mobley et al. 2000, Barlow 2006). The creation of the Hawai‘i catalog was the first photo-identification catalog for this species anywhere in the world and provided a means to closely examine the species’ biology in Hawai‘i. From this catalog, a more accurate, and precise population estimate was generated, along with the ability to examine movements, residency, and population structure. More than 1,600 unique individual melon-headed whales were included in this catalog; associations, re-sightings, and encounter locations were fundamental in providing evidence that there are at least two populations of this species within Hawaiian waters. The Hawai‘i resident and Main Hawaiian Island populations showed a number of important differences in terms of their sighting locations, movements, water depth preferences, and population sizes. The resident population, with an estimated abundance of approximately 450 individuals, was only ever found in shallow waters off the northwest side of the island of Hawai‘i (Figure 2.13). In contrast, the Main Hawaiian Islands population, with an estimated abundance of about 5,800 individuals, was found to move throughout the range of the Main Hawaiian Islands and was most often encountered in deep water (Figure 2.11). These findings greatly improve our understanding melon-headed whales in Hawai‘i, and offer valuable information to further our knowledge of the species elsewhere in the world.

Site Fidelity, Movements, and Behavior

Prior evidence of between-island movements throughout the Main Hawaiian Islands (Huggins et al. 2005) indicated that behavior of melon-headed whales in Hawai‘i more closely resembled the offshore deep water preference of the species described by some (e.g. Mullin 1994), rather than the behavior of the populations described at some oceanic islands (e.g. Brownell et al 2009). Evidence of multiple populations in Hawai‘i, however suggests that both types of patterns are found within one area, with the Main Hawaiian Islands population moving vast distances between islands, and the resident population remaining within a limited range off the northwestern region of the island of Hawai‘i. Shallenberger (1981) noted that 75 – 100 melon-headed whales were consistently seen off the North Kohala Coast, Hawai‘i. It seems plausible that these sightings were of individuals comprising the resident population, and may suggest the presence of this population for nearly three decades or more. That multiple populations of the same species can occur in adjacent, and even overlapping waters, suggests that each population is taking advantage of different foraging niches and perhaps also exhibiting dissimilar social organization and behavior. In Brownell et al.’s (2009) review of melon-headed whale occurrences and behavior near oceanic islands they note a possible resident community off the island of Mo‘orea in French Polynesia, based on photo-identification of more than 100 individuals in the area (Brownell et al. 2009). Preliminary photo-identification results for melon-headed whales off Palmyra Atoll also suggest at least some degree of site fidelity based on re-sightings (Baird et al. unpublished). Diurnal resting behavior was typical at several island locations; for instance, melon-headed whales near Palmyra Atoll remained in the shallower waters (about 400 m) close to the reef line during the day and moved offshore to deeper waters (up to 1,300 m) in the late afternoon (Brownell et al. 2009). Similar observations also occurred

at Nuku Hiva in French Polynesia (Brownell et al. 2009) and near Dominica in the Caribbean (Watkins et al. 1997).

Variability in both behavior and social structure has been shown for different populations of spinner dolphins in the Hawaiian Archipelago (e.g. Norris 1994, Karczmarski et al. 2005), and there is no reason to believe other species would not also exhibit such differences. Andrews et al. (2006, 2010) further showed genetic diversity between populations of spinner dolphins off each of the Main Hawaiian Islands and throughout areas of the Northwestern Hawaiian Islands. Photographic data on bottlenose dolphins in Hawai‘i showed high site fidelity to specific island regions, along with an absence of movement between islands (Baird et al. 2009). Rough-toothed dolphins off the island of Hawai‘i showed high site fidelity through frequent re-sightings (Baird et al. 2008a). Re-sighting rates were lower for rough-toothed dolphins seen off the islands of Kaua‘i/Ni‘ihau, and only two instances of between-island movements were recorded from these individuals, suggesting the possibility for multiple stocks for this species in Hawai‘i (Baird et al. 2008a). Off Kaua‘i, rough-toothed dolphins were found in larger groups and in shallower waters (Baird et al. 2008a), so like melon-headed whales, differences between stocks were shown through multiple lines of evidence. Both genetic and photographic evidence has shown that multiple populations of false killer whales occur in Hawai‘i: a near-shore insular stock, and an offshore stock (Chivers et al. 2007, Baird et al. 2008b). With so much variability in range and movements of odontocetes—both on a global scale, and in Hawai‘i, it should come as no surprise that melon-headed whales are behaving differently than each of the other species in Hawai‘i that have been studied in recent years.

The Hawai‘i resident population exhibited high site fidelity over a relatively limited range (Figure 2.13). The Main Hawaiian Islands population exhibited some site fidelity (given

the re-sighting information); however, animals from this population utilized an expansive range, encompassing at least the 600 km that stretch from Kaua‘i/Ni‘ihau to the island of Hawai‘i (Figure 2.11). Schorr et al. (2009) showed a highly variable range of movements via satellite data for melon-headed whales tagged off the island of Hawai‘i. Further support for this resident population comes from satellite information of two individuals tagged during two separate encounters; both individuals, linked to the resident population, stayed within close proximity to their original tagging locations while most other individuals tagged from the Main Hawaiian Islands population moved great distances (Schorr et al. unpublished). While such vast movements were shown to occur over relatively short periods of time through the satellite data, vast movements were also confirmed via photographic evidence. Several individuals seen in April 2008 off the island of Hawai‘i were re-sighted two months later in June 2008 off the island of Kaua‘i. These two island regions represent the furthest two points of the Main Hawaiian Islands and the areas that there are photos available. Several of the same individuals who were re-sighted off Kaua‘i were also seen again in December 2008 off the island of Hawai‘i. Most recently, four encounters from the Pacific Islands Fisheries Science Center (PIFSC) off O‘ahu between October 2 – 15, 2009, contained individuals who were last seen in the April 2008 encounter off Hawai‘i, the June 2008 encounter off Kaua‘i, and individuals seen four years previously off Hawai‘i. Clearly, movements seem to occur frequently, and often over a wide range, for individuals comprising the Main Hawaiian Islands population. Such re-sightings suggest that both populations exhibit site fidelity – the residents to a limited range off the northwest side of the island of Hawai‘i, and the Main Hawaiian Islands population to the expansive 600 km linear range that encompasses the Main Hawaiian Islands.

Mark-Recapture: Interpretation, Assumptions, and Bias

Individual encounter histories used in the mark-recapture analyses were compiled using only good or excellent quality photographs (Figure 2.2) of distinctive or very distinctive individuals (Figure 2.3) to minimize the likelihood of missing matches. The possibility of missed matches due to mark change is low, given the rate of mark changes (one mark change every 6.7 – 10.3 years), as was the possibility of missed matches due to human error; although both scenarios likely resulted in some positive bias to the populations estimates.

Not all individual melon-headed whales were available for re-sighting; over the duration of this study, there were likely a number of births and deaths that occurred, as well as the possibility of immigrations or emigrations. It was therefore appropriate to use an open population model to estimate the abundance of melon-headed whales in Hawai‘i. As stated previously, Jolly-Seber type mark-recapture analyses make several assumptions about the data being analyzed. The first assumption, that every marked animal present in the population has the same probability of recapture, may be the assumption that is most often violated. The violation of this assumption, also known as “heterogeneity of recapture,” occurs due to inherent differences in individual animals (Hammond 1986) and can result in either a positive or negative estimate of abundance depending on the circumstances. Capture heterogeneity is thought to be widespread in the animal kingdom (Pradel et al. *In Press*), and in cetacean mark-recapture methods, it most often causes a negative bias. In terrestrial mark-recapture studies, such heterogeneity of recapture can be thought of as individuals that are either “trap-happy” (animals more likely to be caught in a trap, i.e. captured) or “trap-shy” (animals less likely to be caught in a trap). The same idea can be carried over to mark-recapture work with free-ranging cetaceans. There may be some individuals more likely to approach a boat

closely, and therefore be photographed, and some individuals who are more likely to stay further away from a boat, and be less likely to be photographed. In encounters with a small number of individuals, such avoidance or affinity may be apparent to the photographers trying to photograph all individuals; however, with encounters that involve a large number of individuals, this may be less apparent at the time. As with terrestrial animals who are trap-happy or trap-shy, age, sex, and previous experiences may all play a role in how close a given individual gets to a boat, and how likely it is to be “captured.” Such responses can cause biases to population estimates. Trap-happy animals can cause a negative bias, whereas trap-shy animals can cause a positive bias (Pollock and Alpizar-Jara 2005). It is possible that either of these scenarios may have occurred, which would reduce our confidence in the population estimates; however, methodology during the directed field efforts attempted to minimize this bias by repeatedly moving through groups of melon-headed whales with multiple photographers attempting to obtain photos of all individuals present. Pooling data for both the full encounter history of all animals should have also helped to reduce heterogeneity of capture in this analysis; however, in pooling the data, a large portion of encounter histories are lost, and therefore insufficient data existed to perform all program RELEASE tests on this subset.

If some animals exhibit greater movements than others, this can also lead to heterogeneity of capture probability and can consequently affect abundance estimates (Larsen and Hammond 2004). Given the restricted range of the Hawai‘i resident population, including these individuals into an estimate of population size combined with the Main Hawaiian Islands population would introduce significant spatial heterogeneity. As a result, it is more appropriate to interpret the mark-recapture results as two separate estimates, one for the resident population and one for the Main Hawaiian Islands population.

Violation of the second assumption, that all marked individuals have an equal chance of survival, usually causes a positive bias for abundance estimation; however, this assumption is more likely to be violated when animals are physically handled for marking (as in terrestrial studies), or when marking does not equally represent all age classes. For example, in many terrestrial animals, it is the younger animals that are more prone to capture; therefore, juvenile survivorship, which may be significantly less than adult survivorship, may be over-represented. As dorsal markings tend to accumulate with age, the opposite trend may be accentuated in such photo-identification data; however, the ability to incorporate the unmarked portion of the population is believed to alleviate the potential for such violations.

The third assumption is that marks are not lost or missed. Mark loss can result in upward bias for abundance estimation (Wilson et al. 1999). New nicks and/or notches on non-distinctive or slightly distinctive individuals would have been more likely to have been missed than those on individuals already considered distinctive. The inclusion of only the distinctive and very distinctive individuals in the mark-recapture analysis should have helped control for this problem. There were likely some matches, however, that were missed based on major dorsal fin mark changes, especially for sighting histories that spanned the course of several years. Despite the low rate of known mark changes, violations of this assumption may have caused a small upward bias to the population estimates. Additionally, some matches were missed, even without mark changes having occurred; therefore, re-sightings may be underrepresented. In an attempt to maintain quality control, an additional experienced matcher took cataloged individuals through the catalog a second time. Approximately 8% of individuals were found to have already been cataloged identifications; this would result in a positive bias to the population estimates.

An additional number of missed matches were found opportunistically throughout the cataloging process and reflects that the catalog continues to be a work-in-progress.

The final assumption is that all samples are instantaneous; in other words, the population size does not change during the sampling event. Estimates could be positively or negatively biased by the violation of this assumption, depending on whether the majority of samples occurred towards the beginning or the end of a sampling period. Individuals sampled at the end of a sampling period may have a greater probability of survival compared to individuals sampled towards the beginning of a sampling period. Although this was a long-term study encompassing six years of data, melon-headed whales are a long-lived species, and therefore the effects of a violation of this assumption should be small. While there is no information to assess whether the population has increased or decreased over this period, there have been no reported mass strandings or die-off events.

In summary, of the four Jolly-Seber assumptions, equal catchability and mark loss were the most likely to have been violated. When average capture probabilities are high (≥ 0.50), heterogeneity becomes less important (Pollock et al. 1990). While neither the Hawai‘i resident nor the Main Hawaiian Islands populations had such high capture probabilities, re-sighting rates were higher for the resident population, and therefore this bias may be less prevalent in the estimate for this population. While an effort was made to reduce heterogeneity of capture through pooling of the data for the full dataset, this came at a cost, and even then it could not be eliminated completely. When attempting to pool data for the Main Hawaiian Islands population, so many encounter histories were lost that there was not enough information for program RELEASE to run all tests. Model validity therefore could not be established, and the full encounter histories for these individuals were used instead. The population estimates which

make the most biological sense, the Hawai‘i resident and Main Hawaiian Islands populations, may show some negative bias if heterogeneity of capture was indeed problematic and likely *do* reflect a positive bias based on missed matches. Comparing the results of TEST 2 for the resident and Main Hawaiian Islands populations suggest that heterogeneity was more of a concern with the Main Hawaiian Islands population, which comes as no surprise given that the full encounter histories had to be used in order to check for model validity.

In light of the discovery of the Hawai‘i resident population (and besides no longer making sound biological sense), there are additional deterrents from using the annual dataset that encompassed all identifications. Pooling the data created extremely sparse re-sighting information, which prevented a proper analysis of goodness of fit. Inclusion of subsequent encounters (i.e. unprocessed data from 2009 forward) would greatly benefit the accuracy of such analyses by providing the possibility of re-sighting information for the 2008 identifications. Furthermore, precision and bias correlate with the longevity of a data set; additional encounter histories would allow for more precise and less biased estimates (Hammond 1990).

Despite the high precision in all of the presented population estimates, they should nevertheless be interpreted cautiously. Lebreton et al. (1992) remind us that models do not provide reality; rather, they provide the best representation of the data for a given purpose. Despite their limitations, these estimates are improvements on the current abundance estimates available for melon-headed whales in Hawai‘i and provide a baseline from which we can work to continue to increase our understanding of the species with regards to population size and trends.

Were Field and Photographic Efforts Sufficient?

With the exception of Kaua‘i/Ni‘ihau, survey efforts were limited to the leeward sides of each island region. Sightings of melon-headed whales did occur off the windward side of Kaua‘i, and given satellite data showing vast movements of some individuals away from their initial tagging locations (Schorr et al. 2009), it is possible that at least some animals are in fact using all waters surrounding each of the islands. Across all island regions and assessing only the well-photographed, distinctive individuals, there were 1,515 identifications of 1,046 melon-headed whales inclusive of 469 re-sightings of 330 individuals. These numbers are based on 18,115 photographs that have been fully processed, and excluding the initial catalog, reflect at least 1,400 hours of dedicated photo sorting/matching effort on behalf of the author, as well as nearly 500 hours of sorting assistance. The remaining 13,296 photos were only partially processed (9,303 fully sorted and partially matched, 3,993 partially sorted and partially matched). With the 2009 field season, additional photos were taken; however, these were only examined briefly to ensure that matches to one of the main populations existed. Continued matching of the remaining photos would likely show, as indicated in the discovery curves (Figure 2.17), that the number of identifications and re-sightings will continue to grow. The number of identifications per island was proportional to the amount of field effort conducted in each region, with the most identifications from island of Hawai‘i (1,067), followed by Kaua‘i/Ni‘ihau (426), and finally O‘ahu (22). With increased effort at other islands, the number of identifications for that island region would likely increase as well. However, documentation of inter-island movements for individuals associated with the Main Hawaiian Islands population suggests that new identifications from other islands would likely link to this group. Therefore, despite the bias in the amount of fieldwork conducted off the island of Hawai‘i, it seems as

though this effort was, at the least, adequate in representing this population. The discovery of the resident population of melon-headed whales using the shallower waters off the northwest side of the island of Hawai‘i came as a surprise, especially considering the generally deep-water preference for this species. The existence of this resident population suggests that there may be other island-associated populations of melon-headed whales in Hawai‘i, but field efforts from this study were unable to detect them. If there are, in fact, other small populations of melon-headed whales exclusively using island-specific niches, these animals may be at greater risk for a number of different localized threats, such as fisheries interactions, anthropogenic noise, and coastal runoff.

Hawai‘i Residents versus Main Hawaiian Islands Population

When comparing and contrasting the Hawai‘i resident population with the Main Hawaiian Islands population, a number of differences were evident. While distance from shore did not vary between residents and the Main Hawaiian Islands population (median 9.40 km compared to 10.05 km respectively), depth of the encounters did (median 381 m compared to 1,844 m). All of the sightings of the resident population were clustered at the northern end of the range for sightings off the island of Hawai‘i, north of Keahole Point. South of this point, water depths drop off quickly close to shore. Encounters with the Main Hawaiian Islands population took place in much deeper water, whereas the habitat range for the resident population occurred over a shallow plateau (Figure 2.28). Of course, all sightings took place during the daytime/daylight hours (range 07:33 – 17:58), so whether movements further offshore, towards the deeper ‘Alenuihāhā Channel (maximum depth ~1,900 m) occurred at nighttime for individuals of the resident population would have to be assessed through satellite data. Two individuals from

the resident population were tagged, and preliminary analysis of this data does suggest that offshore nighttime movements may be taking place (Schorr et al. unpublished). Spinner dolphins in Hawai‘i have been shown to undergo nightly movements offshore to feed on a vertically migrating prey layer (Benoit-Bird et al. 2003) and diel acoustic patterns of melon-headed whales at Palmyra Atoll suggest that feeding is most likely occurring at night (Baumann-Pickering 2009).

While associations with other species occurred for both the Hawai‘i resident and Main Hawaiian Islands population, the species they were found associating with were completely different. The only species the resident population was seen associating with were humpback whales. Given that humpback whales only occupy Hawaiian waters during the winter months (typically December through April), this association was seen in two out of the possible seven “winter” occasions. Humpback whales migrate to Hawai‘i to utilize the warm, shallow waters as their breeding grounds, and some of the shallowest waters off the island of Hawai‘i are in the same location as the resident population. In one of the two encounters with the humpback whales, several of the melon-headed whales were closely associating with the humpbacks (Figure 2.29).

The Main Hawaiian Islands population of melon-headed whales was seen associating with or near a broader range of species, including six sightings with rough-toothed dolphins, three sightings with short-finned pilot whales (Figure 2.6), one sighting with pantropical spotted dolphins, one sighting with killer whales (albeit fleeing from them, see Baird et al. 2006), and one sighting with Fraser’s dolphins. Of 26 encounters with the Main Hawaiian Islands population, ten were mixed encounters with at least one other species present. Like these melon-headed whales, each of the associated species also shows some preference for a deep water

habitat (e.g. Baird et al. 2008a, Baird et al. 2003, Reeves et al. 2002). It is possible that it may be more advantageous for the more oceanic species to aggregate for predatory avoidance.

Differences in the proportion of distinctive individuals between the Hawai‘i resident and the Main Hawaiian Islands populations were slight, ranging from 53.4 – 62.0 (median = 57.7, CV = 0.11; n = 2) for the resident population, and from 59.5 – 64.0 (median = 61.9, CV = 0.03; n = 4) for the Main Hawaiian Islands population. Based on the extremely small sample sizes and similar values for both populations, combining all encounters examined to produce an overall distinctiveness rating for all melon-headed whales in Hawai‘i seems appropriate. The overall percentage of distinctive and very distinctive individuals therefore ranged from 53.4 – 64.0 (median = 61.8, CV = 0.06; n = 6). This percentage of distinctiveness is less than other species in Hawai‘i, such as pygmy killer whales (median = 73.2%) (McSweeney et al. 2009), false killer whales (mean = 73.7%, SD = 22.8%) (Baird et al. 2008b), common bottlenose dolphins (median = 80%) (Baird et al. 2009), and rough-toothed dolphins (median = 100%) (Baird et al. 2008a). Kiszka et al. (2008) reported that 81% of melon-headed whales around the Mozambique Channel Island of Mayotte were “identifiable” (i.e. had any markings). A comparable calculation from Hawai‘i, including those rated slightly distinctive, results in a median “identifiable” percentage of 84.9%, similar to the findings of Kiszka et al. (2008).

Mark changes were evident from individuals of both populations; however, the number of individuals with mark changes from the Hawai‘i resident population was higher than that of the Main Hawaiian Islands population (Table 2.2). This could be a result of the more complete sighting histories for resident individuals (i.e. it is more likely that mark changes were detected with the residents) or, alternatively, individuals of the Main Hawaiian Islands population may be less likely to undergo mark changes. Nicks and notches along the dorsal fin are known to occur

both naturally (e.g. through conspecific interactions) as well as from anthropogenic sources (e.g. line entanglements). Attributing the cause of any dorsal fin mark or injury will almost always carry with it a high degree of uncertainty; however, the source of some injuries may be more apparent than others. Dorsal fin disfigurements were present on individuals of both populations, suggesting that fisheries interactions occur throughout both ranges, although of the 50 individuals that had dorsal markings suggestive of line or rope entanglement, only 11 individuals were from the resident population. It therefore does not seem that the higher proportion of mark changes is due to line or rope entanglement. Presumably, individuals from the Main Hawaiian Islands population may spend more time travelling than individuals from the resident population, and therefore less time resting and/or socializing. If this is the case, the higher number of mark changes for the residents may be indicative of greater conspecific interactions. Further dedicated research would be needed to assess this.

For all individual melon-headed whales, mark changes were estimated to occur on average once every 9.2 – 13.8 years; although, given the higher number of re-sightings for the Hawai‘i resident population, the estimated occurrence of mark changes for the residents (once every 6.7 – 10.3 years) may be more accurate than the overall rate of mark changes. The rate in which mark changes occurred for other small odontocetes in Hawai‘i was calculated in several more lengthy studies, similar to this one. For rough-toothed dolphins, mark changes occurred on average once every 2.42 years (Baird et al. 2008a). In pygmy killer whales, a mark change occurred every 3.9 – 6.1 years (McSweeney et al. 2009), and false killer whales underwent a mark change every 6.9 – 8.8 years (Baird et al. 2008b). In general, mark change occurrence for melon-headed whales in Hawai‘i was less frequent than rough-toothed dolphins and pygmy killer whales, and was most similar to the frequency for false killer whales. These results would be

anticipated based on the percentage distinctive for each species; the greater the percentage distinctive, the more frequently mark changes would be expected to occur.

Resident Population: Why so Shallow?

Why would one population of melon-headed whales choose to use a shallow water habitat while their conspecifics primarily utilize the adjacent deeper offshore waters? The answer may lie in the productive waters between the islands of Hawai‘i and Maui/Kaho‘olawe, an area separated by the ‘Alenuihāhā Channel (maximum depth ~1,900 m) (Figure 2.28). In this area, northeasterly trade winds are accelerated and funneled between the islands due to their steep topography, and result in the formation of cyclonic eddies. Nowhere else in Hawai‘i are these highly productive mesoscale features more prominent than the ‘Alenuihāhā Channel (Seki et al. 2001). Cyclonic eddies, or cold ring eddies, cause upwelling of cool waters (Figure 2.30), and are ‘hotspots’ for biological and physical activities. The rising of the cool waters creates physical gradients in the ocean that predators can use to locate accompanying aggregations of prey (Seki et al. 2001). Fishermen can use also utilize these same cues to find fish, thereby increasing the likelihood of overlap between humans and melon-headed whales (as well as other predators, such as birds, fish, or turtles, tracking these features), and increasing the potential for interactions with fisheries. A 1995 study of cyclonic eddies occurring over the course of the Hawai‘i International Billfish Tournament (HIBT) found that eddy location overlapped with areas of high tournament fish catches (Seki et al. 2001). A recent analysis of offshore movements of satellite tagged melon-headed whales in Hawai‘i (i.e. non-residents) showed that

these animals were found in association with both the edges of cyclonic eddies and the centers of the warm anticyclonic eddies (Woodworth et al. *submitted*).

Brownell et al. (2009) noted that although quantitative data was lacking, reports of melon-headed whales near some oceanic islands were seasonal. The resident population off Hawai‘i was observed in seven of 12 months (February, March, April, July, September, October, and December). Despite less prevalent trade winds driving eddy formation during the summer months (June – August), productive waters off the island of Hawai‘i are maintained year-round through oceanographic influences driven by the presence of the islands themselves (e.g., Doty and Oguri 1956, Gilmartin and Revalante 1974). Given there was seasonal variation in effort, the Hawai‘i resident population presumably would show year-round residency with further sightings based on the presence of these oceanographic features.

Pre-Study Re-Sightings and Long-Term Fidelity

Although the focal period of this study was between 2000 and 2009, re-sightings of individual melon-headed whales from the island of Hawai‘i dated as far back as 1986, suggesting long-term use of this area. The longest and most comprehensive re-sighting spans more than 20 years, and comes from a member of the Hawai‘i resident population, HIPe1579, who was seen in 1986, 1996, 2005, 2006, and 2008 (Figure 2.18). As marks tend to accumulate with age, the distinctiveness of this individual in 1986 suggests that at the time it was a mature adult, and therefore, this animal is likely to be at least in its thirties. The oldest known melon-headed whale based on aging using dentinal growth layers was a 44.5-year old female from a mass stranding in Japan (Miyazaki et al. 1998). From this same group, the oldest male was 38.5 ($n = 75$ males, $n = 44$ females). It is not uncommon for mammalian females to live longer than their male

counterparts (Viña et al. 2005). HIPE1579 was seen on five occasions between 1986 and 2008; in four of these occasions, the animal was swimming alongside other seemingly large, well-marked individuals, suggesting that these were male (Miyazaki et al. 1998) associates (the fifth occasion in 2008 the animal was photographed alone). There were never any calves or otherwise clean-finned individuals which would be more suggestive of a female's associations; therefore, it can be hypothesized that this is, in fact, a long-lived male.

Dorsal Fin and Bodily Injuries

Approximately 62% of individuals within-groups were considered to be “distinctive” or “very distinctive.” Dorsal fin markings tend to accumulate with age; therefore, individuals categorized as “slightly distinctive” or “not distinctive” would likely be predominately younger animals. A number of dorsal and bodily injuries were documented on melon-headed whales over the course of this study. For many cetacean species, nicks and notches along the trailing edge (and sometimes leading edge) of the dorsal fin occur naturally throughout an animal’s lifetime; often through interactions with conspecifics or predators. Some dorsal injuries, however, may be considered human-induced, whether indirectly (i.e. derelict fishing gear), or directly (i.e. gunshot wound, ship strike, or propeller strike). One of the more common dorsal injuries documented were injuries suggestive of line entanglements (Figure 2.21). At least four fishing vessels were seen trolling through groups of melon-headed whales in the Main Hawaiian Islands and may be one possible source of such injuries. In Mayotte, a number of small odontocete species, including melon-headed whales, were also shown to have dorsal fin disfigurements likely caused by fishing line (Kiszka et al. 2008). While entanglement injuries are indirectly

associated with fisheries, the depredation of fishing gear may occasionally elicit a more direct consequence – being shot at; several individuals showed dorsal fin injuries that suggest this may have occurred (Figure 2.23). In the past, some fishermen in Hawai‘i have admitted to resorting to such measures to deter various small odontocetes from stealing their bait or catch (Kuljis 1983; Anonymous 1997). As dorsal fin wounds are long-lasting, and melon-headed whales are long-lived, shooting injuries may have occurred when the practice was more common, although it is also possible that the injuries are more recent, and despite being illegal, such measures continue.

Ship strikes and small vessel collisions have been responsible for numerous deaths and injuries to many cetaceans, most famously, the highly endangered North Atlantic right whale (*Eubalaena glacialis*) (e.g. Knowlton and Kraus 2001). While the number of reports for the smaller odontocetes is much less than those reported for the larger baleen whales, it is possible this may be partially due to limited monitoring and reporting, as well as the scarcity of records from many regions (Van Waerebeek et al. 2007). Large vessel traffic around the Main Hawaiian Islands comes predominately from freighter ships. It would be expected that large vessel collisions with melon-headed whales, or other small species, would more likely be fatal. The Main Hawaiian Islands are also home to a large fleet of smaller recreational and fishing boats. Interactions with these smaller boats could cause severe injuries that may or may not be fatal. In one study in Sarasota Bay, Florida, at least four bottlenose dolphins survived boat strikes, but sustained injuries, as well as dorsal fin and bodily disfigurements (Wells and Scott 1997). In Hawai‘i one individual melon-headed whale from the Main Hawaiian Islands population showed parallel scarring that may have been caused by a propeller (Figure 2.24). While both rake marks and propeller injuries can result in parallel line scarring, rake marks appear closer to one another

than a propeller injury would. For many odontocetes, rake marks have been documented to be a natural part of intraspecific interactions (e.g. Scott et al. 2005), although they may also occur from interspecific interactions.

Additional Information Extracted from Photographic Data

The animal seen on the most occasions was HIPe0657, a female seen eight times, and often with calves. Due to their lack of distinctiveness and the typical long duration between encounters in this study, nursing duration and survival histories of calves cannot easily be determined through existing photographic data; however, eight re-sightings of a mature female does provide a solid foundation for interpreting valuable reproductive information from free-ranging melon-headed whales. Although speculative, sighting history for HIPe0657 may allow inferences on possible birthing intervals. Given her history, it seems possible that in late 2005 or early 2006 she gave birth, and that calf stayed with her for an unknown period of time, although possibly as late as December, 2008. She may have been pregnant in December 2008, and the calf seen in 2009 may have been a yearling. This could suggest an interbirth interval (IBI) of about 3 years. Reproductive information for melon-headed whales is known primarily from analyses of dead (usually stranded) individuals. From 119 animals that stranded off the coast of Japan in January 1982, 39 of 44 females were examined, of which 34 were sexually mature; 13 of these were lactating, 10 were pregnant, and 11 were parous females (Miyazaki et al. 1998). Despite the number of lactating females, no newborn or small calves less than 2.09 m were identified, suggesting either the small calves may have become separated before or during the stranding and/or large calves (those greater than 2.09 m) were still nursing. While Miyazaki et

al. (1998) did not directly report IBI, they estimated the annual ovulation rate to be 0.28, which could suggest an IBI around 3.6. In an assessment of a variety of reproductive parameters that included 58 cetacean species, no known IBI was provided for melon-headed whales, although many other small odontocetes had an IBI ranging from 3.0 – 4.0, including striped dolphins, spinner dolphins, pantropical spotted dolphins, Atlantic spotted dolphins (*Stenella frontalis*), Clymene dolphins (*Stenella clymene*), Atlantic hump-backed dolphin (*Sousa teuszii*), common bottlenose dolphins (from both the Atlantic and the Pacific), and Indian Ocean bottlenose dolphins (*Tursiops aduncus*) (Taylor et al. 2007). Further information is required to confidently assign an IBI for melon-headed whales; however, frequent re-sighting information of distinctive free-ranging animals has the potential to contribute to our overall understanding of such parameters.

Future Research

Through directed field efforts spanning a decade, tens of thousands of photographs of melon-headed whales were collected around the Main Hawaiian Islands. These photos have provided a rare opportunity to carry out a long-term scientific study on a species for which few dedicated studies exist. Through a tremendous amount of field work and data processing, answers regarding population size, structure, habitat, and movements of melon-headed whales in Hawai‘i have emerged. This study has shown strong evidence of at least two populations of melon headed whales utilizing the Main Hawaiian Islands – a small, resident population, which appears to exhibit minimal movements over a limited area off the island of Hawai‘i, and a large, Main Hawaiian Islands population, that shows extensive movements as evidenced from between-

island re-sightings. The existence of these two populations was supported by social network analyses, sighting and effort locations, between-island movements (or lack thereof), and habitat use. Mark-recapture population estimates were the first of their kind for melon-headed whales – from any region of the world – and provided estimates with high precision. We have gained valuable information from this work; however, as is often the case in science, in an attempt to answer one question, many new questions have arisen.

The existence of a resident population off the island of Hawai‘i was an unexpected finding and suggests the possibility that there may be resident populations off other islands. Dedicated field efforts are needed to determine whether such populations exist. Continued matching of the available photographic data, genetic analyses, and additional satellite tracking data will provide further information in support of the presence of two distinct populations or provide insight on the possibility of other melon-headed whales that may also be using an overlapping habitat. A more comprehensive examination of social structure for both populations can be obtained through further analysis of the photographic data.

The Main Hawaiian Islands population has showed extensive movements, both through photographic (this study) and telemetry data (Schorr et al. 2009). Currently, the furthest documented re-sightings are of individuals between the islands of Kaua‘i/Ni‘ihau and Hawai‘i, a distance of nearly 600 km. Whether these individuals move even further, perhaps up into the Northwestern Hawaiian Islands, has yet to be determined. Continued satellite tagging of individuals from this population will help establish what limits exist for this population’s home range. As the Northwestern Hawaiian Islands are a protected monument that requires extensive permitting processes, any photographic data that can be provided by those agencies already

conducting field work in the area would be invaluable to learning more about the potential movements of these individuals.

Two recommendations can be made to maximize our understanding of the Hawai‘i resident population that would require minimal funding. The first is to complete the photo-id matching for the remaining encounters in order to catalog as many of the estimated ~450 animals as possible. This would allow for improved monitoring of the population in the future. The second recommendation is to run a closed model mark-recapture analysis on the resulting cataloged individuals (over a short time frame) in order to compare the estimate with the open model population estimate provided in this study. The predictable and limited home range of the resident population may also offer a unique opportunity to closely examine a melon-headed whale population through a dedicated field study, and could provide a wealth of new information on the species. Small populations, such as the Hawai‘i residents, often have significant management concerns, especially when the population has a restricted habitat. The habitat for these individuals overlaps with popular recreational fishing grounds, increasing the possibility for fisheries interactions. The biennial RIMPAC naval sonar training exercises as well as other naval exercises may also occur in waters adjacent to or overlapping with the habitats of both the resident and Main Hawaiian Islands populations (Anonymous 2006), and given the evidence of susceptibility to sound impacts (Southall et al. 2006, Brownell et al. 2009) may pose additional concern. With the discovery of this smaller resident population, a case could be made to implement an exclusion zone encompassing the boundaries of their range to provide increased protection from some of these threats.

No population trend information exists for melon-headed whales anywhere in the world. Long life spans combined with unknown reproductive rates will require continued monitoring to

detect such trends; however, this study can provide a baseline for evaluating population trends in Hawai‘i. Photographic data has played a role in evaluating the growing population trend of humpback whales utilizing the waters of Hawai‘i (Calambokidis et al. 2008), as well as the declining population of false killer whales in Hawai‘i (Baird 2009). Cessation of whaling, combined with protection under both the Marine Mammal Protection Act (MMPA) and the Endangered Species Act (ESA) has likely been the source of recovery for humpback whales in the North Pacific. With the exception of sperm whales, currently, no odontocete inhabiting the waters of Hawai‘i receives added protection beyond the MMPA; however, a false killer whale Take Reduction Team (TRT) has been formed to address bycatch and NMFS is currently considering listing the insular population of false killer whales under the ESA. Talk of increased protection for spinner dolphins has been underway for several years in an attempt to alleviate the number of people swimming with and interacting with the species. One concern is that if regulations are put into place to protect only spinner dolphins, the problem of such human interactions will only be displaced to other species. Due to the shallower and more localized (and predictable) habitat in which the Hawai‘i resident population of melon-headed whales is found, they are one species that could be vulnerable to such interactions.

Tables and Figures

Table 2.1 Number of well-photographed (rated 3 or 4), distinctive (rated 3 or 4) melon-headed whale identifications and individuals by area inclusive of only fully-sorted encounters.

Island area	# IDs of marked individuals	# individuals (excluding within-area re-sightings)	# (%) individuals seen > once	#(%) documented at other islands	# within-area within-year re-sightings	# within-area between year re-sightings	# between-area re-sightings
Kaua‘i / Ni‘ihau	426	316	96 (30.4)	21 (21.9)	87	0	26
O‘ahu	18	18	0	0	n/a	n/a	n/a
Hawai‘i	912	712	154 (21.6)	21 (13.6)	85	112	26
Hawai‘i (residents only)	263	180	64 (35.6)	0	23	60	0
Hawai‘i (excluding residents)	649	532	90 (16.9)	21 (23.3)	62	52	26
All Areas	1356	1046 ^A	250 (23.9)	21 (8.4)	172	112	26

^A Excludes between-area re-sightings

Table 2.2 Frequency of mark-changes for all melon-headed whales in Hawai‘i, the resident population, and individuals of the Main Hawaiian Islands population.

	Cumulative # days between first and last re-sights	Cumulative # years between first and last re-sights	Median # days between re-sightings	Minimum # Mark Changes	Maximum # Mark Changes	Estimated frequency of mark changes (min) (years)	Estimated frequency of mark changes (max) (years)
All Individuals	201,524	552.1	124	40	60	9.20	13.80
Hawai‘i Residents	101,884	279.1	990	27	42	6.65	10.34
Main Hawaiian Islands	99,640	273.0	5	13	18	15.17	21.00

Table 2.3 Summary statistics highlighting model choice, population size estimate (\hat{N} and N), and associated variation for mark-recapture estimates for all identifications, the Hawaii resident population, and the Main Hawaiian Islands (MHI) population obtained using the POPAN parameterization in MARK. AICc = Aikaike Information Criterion, QAICc = Quasi-Aikaike Information Criterion (used when a variance inflation factor of chat = 2.53 was applied), # Par = number of parameters in the model, 95% CI = 95% confidence interval, SE = standard error, CV = coefficient of variation.

Model	AICc	Δ AICc	QAICc	Δ QAICc	Weight	AICc Weight	Model Likelihood	# Par.	\hat{N}	Population Estimation			Corrected for Non-Distinctive Individuals				
										SE	95% CI low	95% CI high	CV	N	95% CI low	95% CI high	CV
<u>All Identifications</u>																	
$\phi(t)p(.)pent(t)$	798.44	0.00	-	-	0.57	-	1.00	7	4,320	359.74	3,615	5,025	0.08	6,990	5,850	8,131	0.10
$\phi(t)p(t)pent(t)$	799.03	0.59	-	-	0.43	-	0.74	12	3,961	762.09	2,468	5,455	0.19	6,409	3,994	8,827	0.20
$\phi(.)p(t)pent(t)$	813.90	15.46	-	-	0.00	-	0.00	7	3,517	336.23	2,858	4,176	0.10	5,691	4,625	6,757	0.11
$\phi(.)p(.)pent(t)$	928.13	129.69	-	-	0.00	-	0.00	6	5,645	520.91	4,625	6,667	0.09	9,134	7,484	10,788	0.11
Weighted average	-	-	-	-	-	-	-	-	4,166	531.39	3,002	5,332	0.13	6,741	4,858	8,628	0.14
<u>HI Resident Population</u>																	
$\phi(.)p(t)pent(t)$	463.84	0.00	-	-	0.72	-	1.00	9	277	22.36	233	321	0.08	448	377	519	0.10
$\phi(t)p(t)pent(t)$	465.74	1.91	-	-	0.28	-	0.39	11	274	22.94	229	319	0.08	443	371	516	0.10
$\phi(.)p(.)pent(t)$	529.44	65.61	-	-	0.00	-	0.00	5	409	42.44	326	492	0.10	662	528	796	0.12
$\phi(.)p(.)pent(t)$	562.73	98.89	-	-	0.00	-	0.00	4	382	43.60	296	467	0.11	618	479	756	0.13
Weighted average	-	-	-	-	-	-	-	-	276	22.52	232	321	0.08	447	375	519	0.12
<u>MHI Population</u>																	
$\phi(t)p(t)pent(t)$	-	-	609.00	0.00	-	1.00	1.00	27	3,581	731.69	2,680	4,483	0.20	5,794	4,337	7,254	0.20
$\phi(t)p(.)pent(t)$	-	-	674.79	65.79	-	0.00	0.00	19	3,090	449.92	2,536	3,645	0.15	5,000	4,104	5,898	0.15
$\phi(.)p(t)pent(t)$	-	-	685.53	76.53	-	0.00	0.00	21	3,505	683.89	2,663	4,348	0.20	5,672	4,309	7,036	0.20
$\phi(.)p(.)pent(t)$	-	-	820.62	211.62	-	0.00	0.00	8	2,382	221.57	2,109	2,656	0.09	3,854	3,413	4,298	0.09

Table 2.4 Program RELEASE goodness-of-fit results for the fully-time dependent ($\phi(t)p(t)pent(t)$) model for the mark-recapture analysis using data from all identifications, the resident population, and the Main Hawaiian Islands (MHI) population. df = degrees of freedom, \hat{c} = variance inflation factor.

All IDs			
Test	Chi-square	df	\hat{c}
TEST 2 + TEST 3	N/A	N/A	N/A
TEST 2	1.02	2	0.51
TEST 3	N/A	N/A	N/A

Residents			
Test	Chi-square	df	\hat{c}
TEST 2 + TEST 3	2.84	8	0.36
TEST 2	2.74	3	0.91
TEST 3	0.11	5	0.02

MHI Population			
Test	Chi-square	df	\hat{c}
TEST 2 + TEST 3	68.27	27	2.53
TEST 2	59.28	12	4.94
TEST 3	8.99	15	0.60



Figure 2.1 Example of survey effort over a 2-week period, December 2009, showing the non-random, non-systematic survey coverage. Each loop represents survey trackline from one day with final survey day highlighted in yellow. From <http://www.cascadiaresearch.org/hawaii/December2009.htm>.

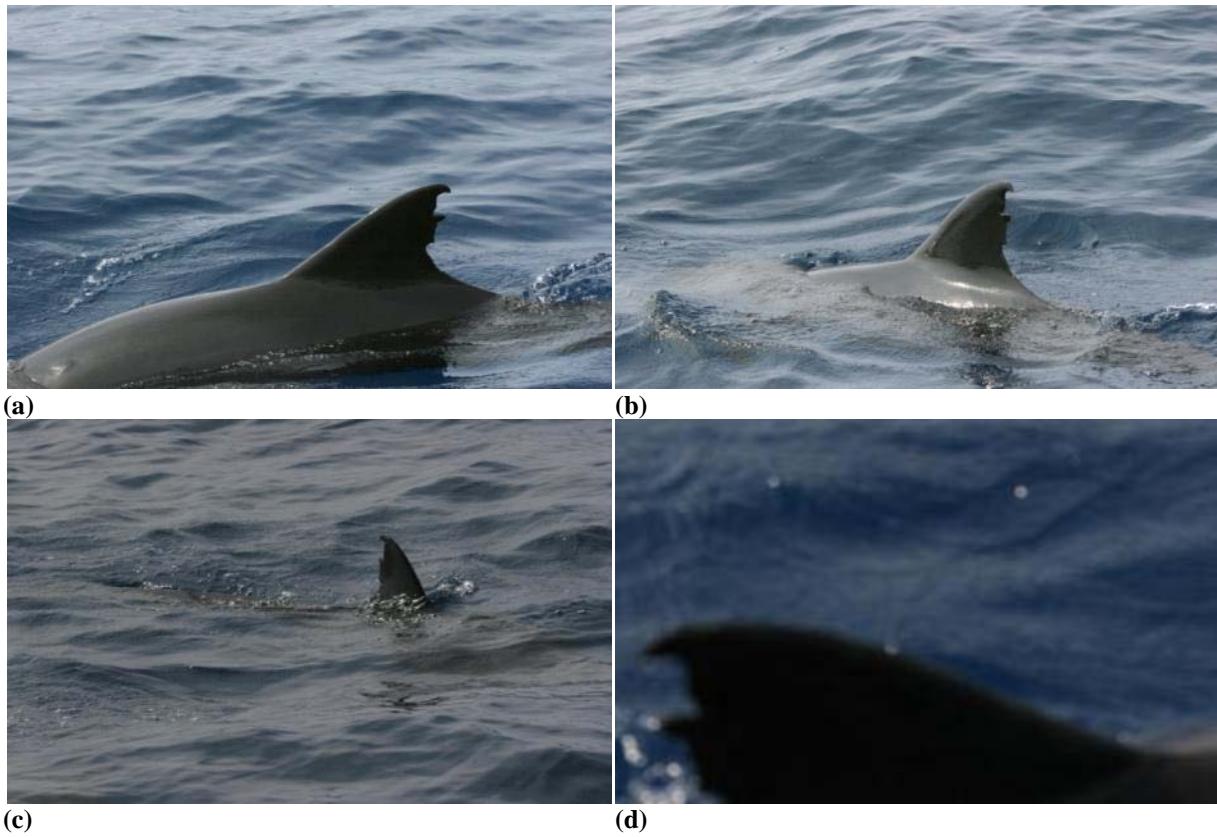


Figure 2.2 Photos of melon-headed whale (catalog no. HIPe0658) showing examples of photo quality (PQ) ratings: (a) PQ rating = 4 (excellent quality); (b) PQ rating = 3 (good quality); (c) PQ rating = 2 (fair quality); (d) PQ rating = 1 (poor quality). All photos ©Cascadia Research Collective; (a) – (d) Jessica Aschettino.

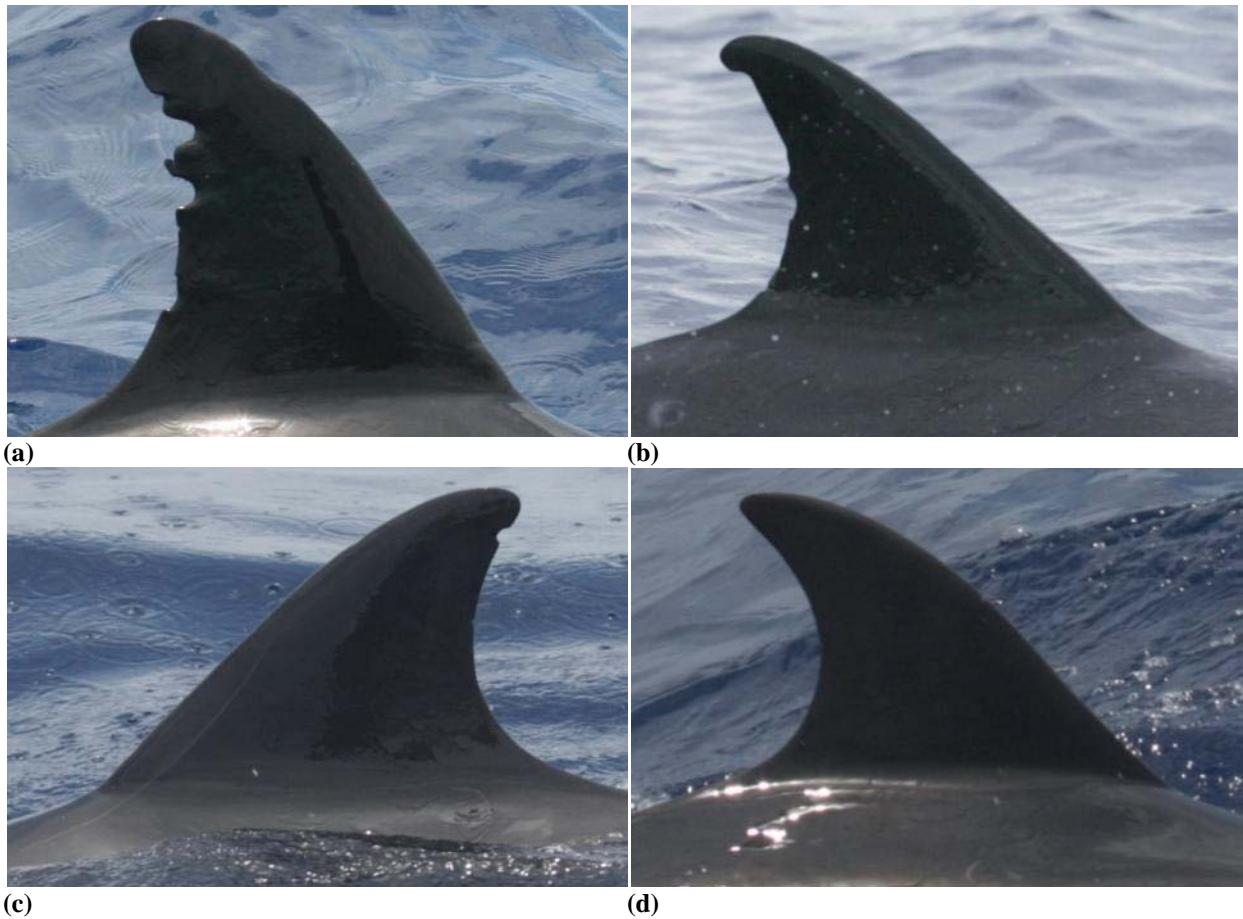
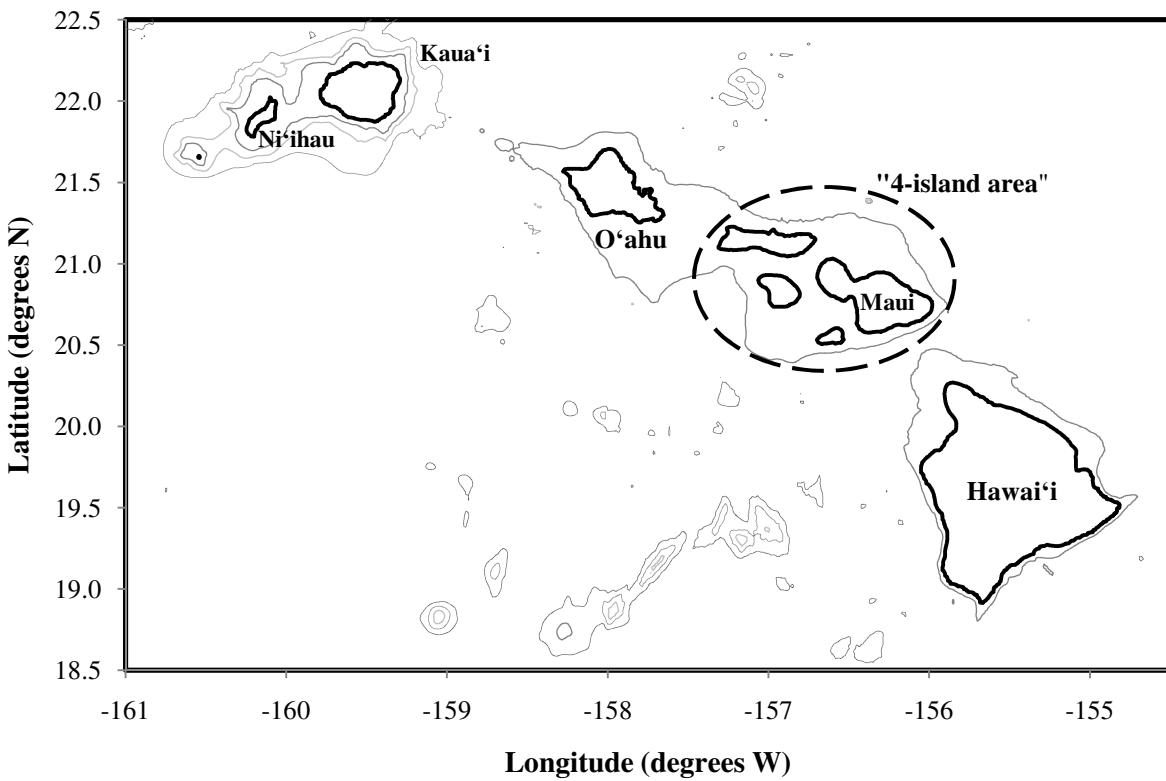


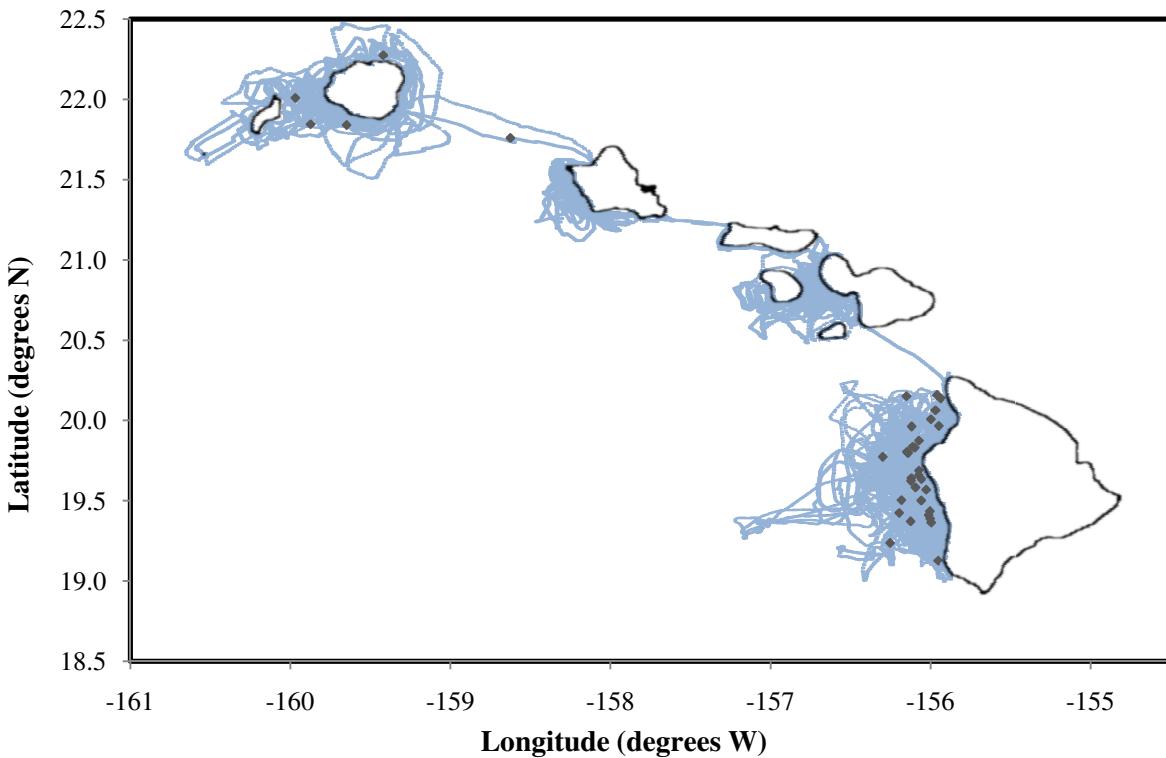
Figure 2.3 Melon-headed whale dorsal fins showing examples of distinctiveness (Dist) ratings: (a) Dist = 4 (very distinctive); (b) Dist = 3 (distinctive); (c) Dist = 2 (slightly distinctive); (d) Dist = 1 (not distinctive). All photos ©Cascadia Research Collective; (a) Darren Roberts (b) Alice Mackay (c) and (d) Annie Douglas.

ID #	2-Feb-05	25-Mar-06	26-Mar-06	30-Mar-06	31-Mar-06	10-Dec-08
HIPe0537	0	0	0	0	1	1
HIPe0538	0	0	0	0	1	0
HIPe0539	0	0	0	0	1	0
HIPe0540	0	0	0	0	1	0
HIPe0628	0	0	1	0	0	0
HIPe0651	0	1	0	0	0	0
HIPe0652	1	1	0	0	0	0
HIPe0653	1	1	0	1	0	0
HIPe0654	1	1	0	1	0	0
HIPe0655	0	1	0	1	0	0
HIPe0657	1	1	1	0	0	1
HIPe0658	0	1	0	1	0	1
HIPe0659	0	1	0	1	0	0
HIPe0660	0	1	0	0	0	0
HIPe0661	0	1	1	0	0	0
HIPe0662	0	1	0	0	0	0
HIPe0664	0	1	0	0	0	0
HIPe0665	0	1	0	1	0	0
HIPe0666	1	1	1	0	0	0
HIPe0667	0	1	0	0	0	0
HIPe0668	1	1	0	0	0	0
HIPe0669	1	1	0	0	0	0
HIPe0670	0	1	0	0	0	0

Figure 2.4 Sample history of 23 resident melon-headed whales prepared for MARK entry. A “0” represents that the individual was not seen and “1” indicates that it was seen.



(a)



(b)

Figure 2.5 (a) Main Hawaiian Islands showing depth contours at 1,000 m, 2,000 m, 3,000 m, and 4,000 m. (b) Effort and sightings of melon-headed whales around the Main Hawaiian Islands: 2000-2009. Survey trackline and sighting locations of melon-headed whales.



Figure 2.6 Mixed sighting of melon-headed whales (foreground) with short-finned pilot whales (background).
Photo ©Cascadia Research Collective, Greg Schorr.



Figure 2.7 Lone individual melon-headed whale showing emaciation (catalog no. HPe0627), **(a)**, discoloration near head and dorsal region, **(b)**, and several large open cookie cutter wounds, **(a)** and **(b)**. Photos ©Cascadia Research Collective; **(a)** Sabre Mahaffy **(b)** Daniel Webster.

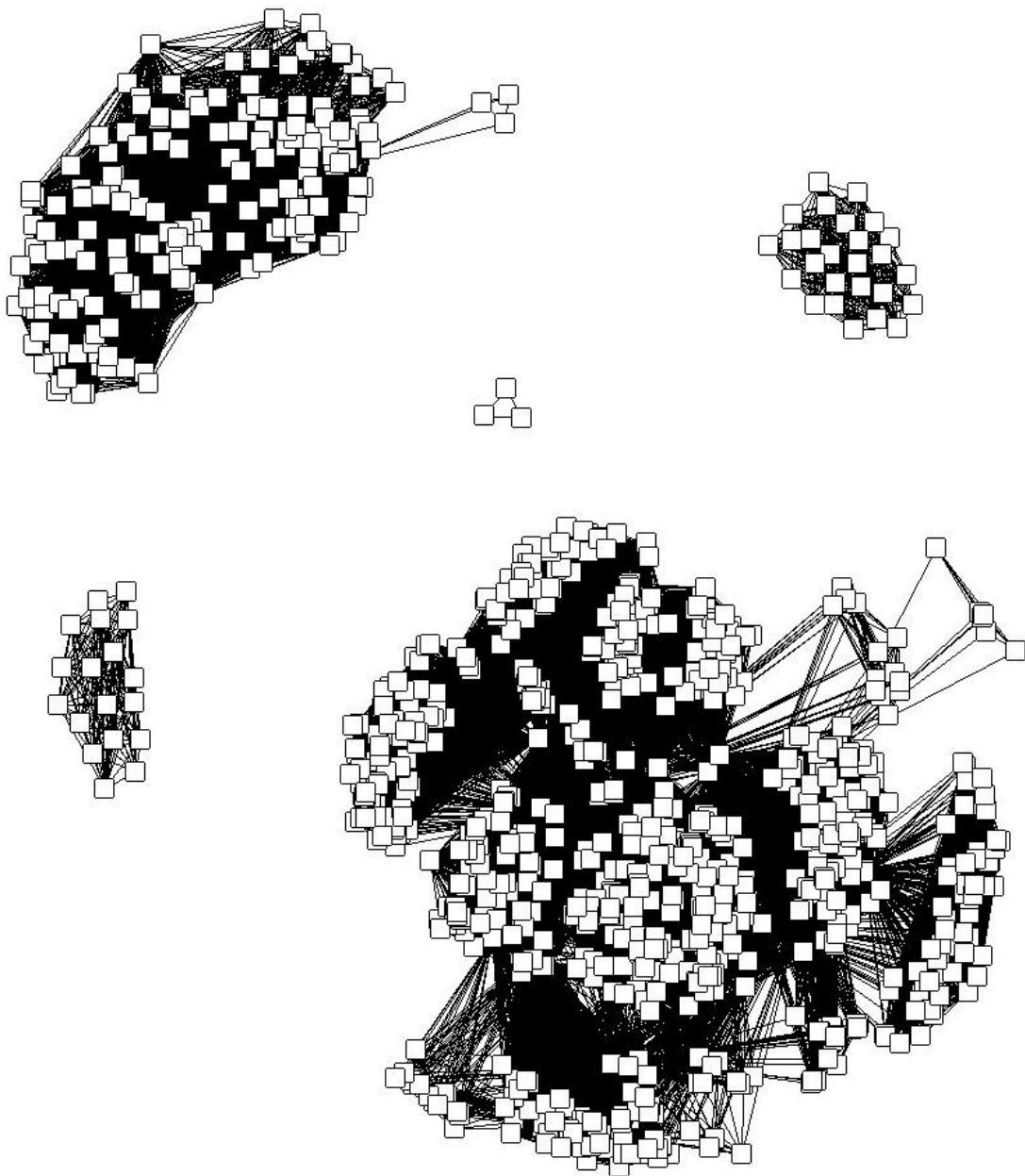


Figure 2.8 Social network diagram showing associations of all well-photographed (rated 3 or 4) distinctive (rated 3 or 4) individual melon-headed whales. Nodes correspond to individual melon-headed whales, and lines between nodes represent presence within the same group. The majority of individuals (820, 78.4%) are linked to the main cluster (Main Hawaiian Islands population), 180 (17.2%) are part of a second large cluster (Hawai'i Island resident population), and the remaining 46 (4.4%) are part of three small clusters not linked to either of the main clusters (a cluster of three seen off Hawai'i, a cluster of 18 seen off O'ahu, and a cluster of 25 seen off Hawai'i).

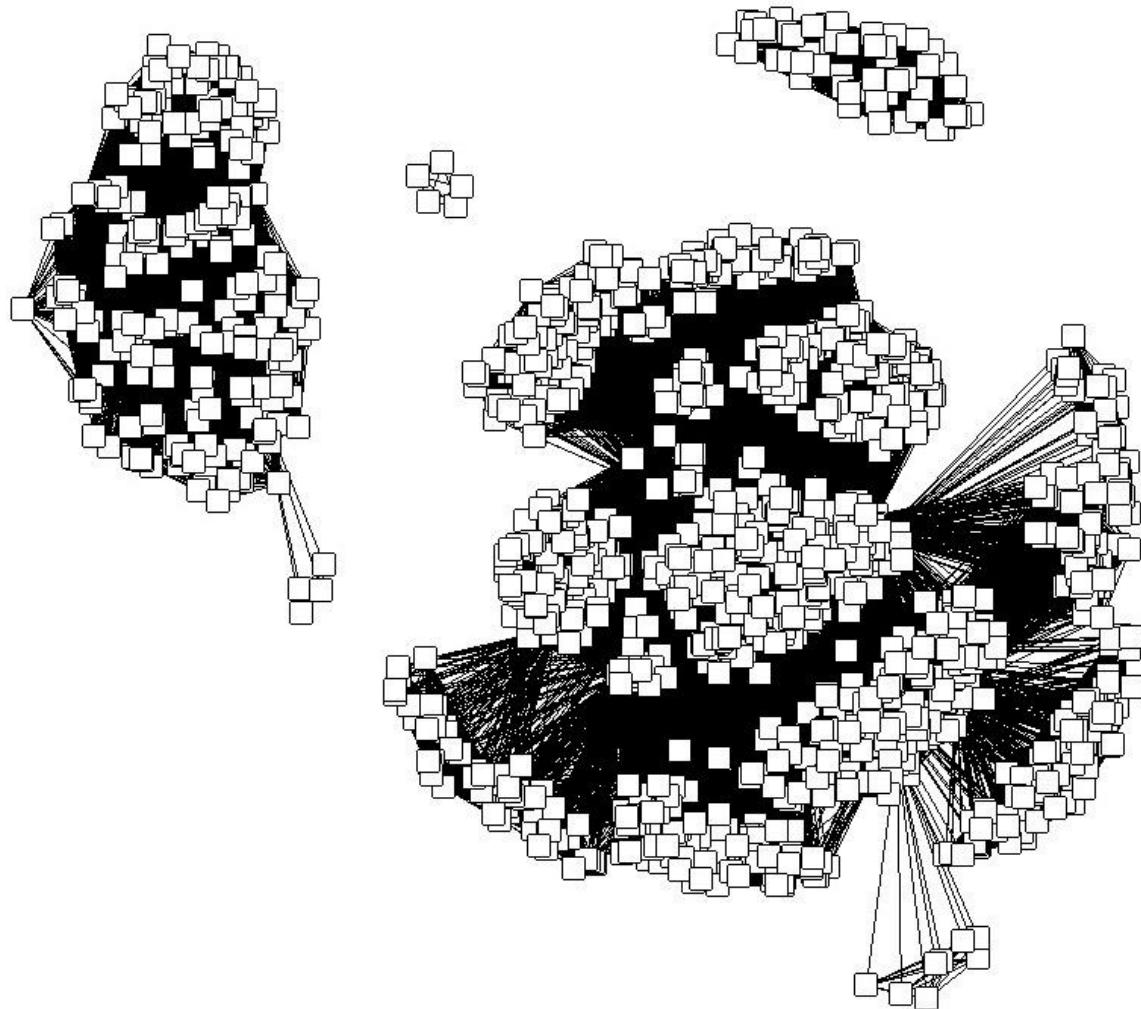


Figure 2.9 Social network diagram showing associations of melon-headed whales when loosening analysis restrictions to include fair quality photographs and slightly distinctive individuals. Nodes correspond to individual melon-headed whales, and lines between nodes represent presence within the same group. The majority (81.1%) are linked to the main cluster (the Main Hawaiian Islands population), 15.4% are part of a second large cluster (the Hawai'i Island resident population), and the remaining 3.5% are part of two small clusters not linked to either of the main clusters (both seen off the island of Hawai'i).

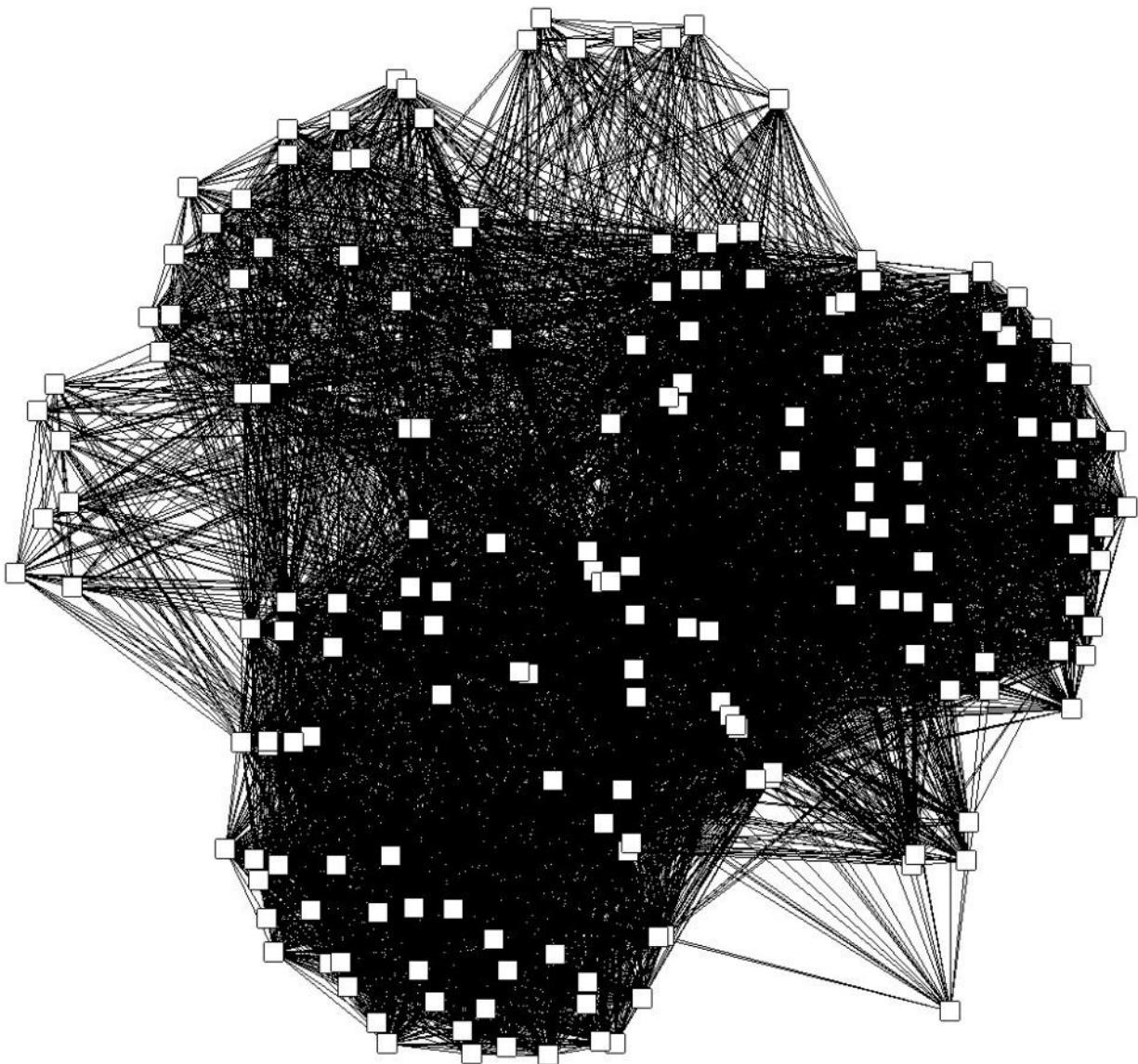


Figure 2.10 Social network diagram showing associations of 180 well-photographed distinctive individual melon-headed whales from six encounters comprised of the second to largest main cluster (i.e. residents). Nodes correspond to individual melon-headed whales, and lines between nodes represent presence within the same group.

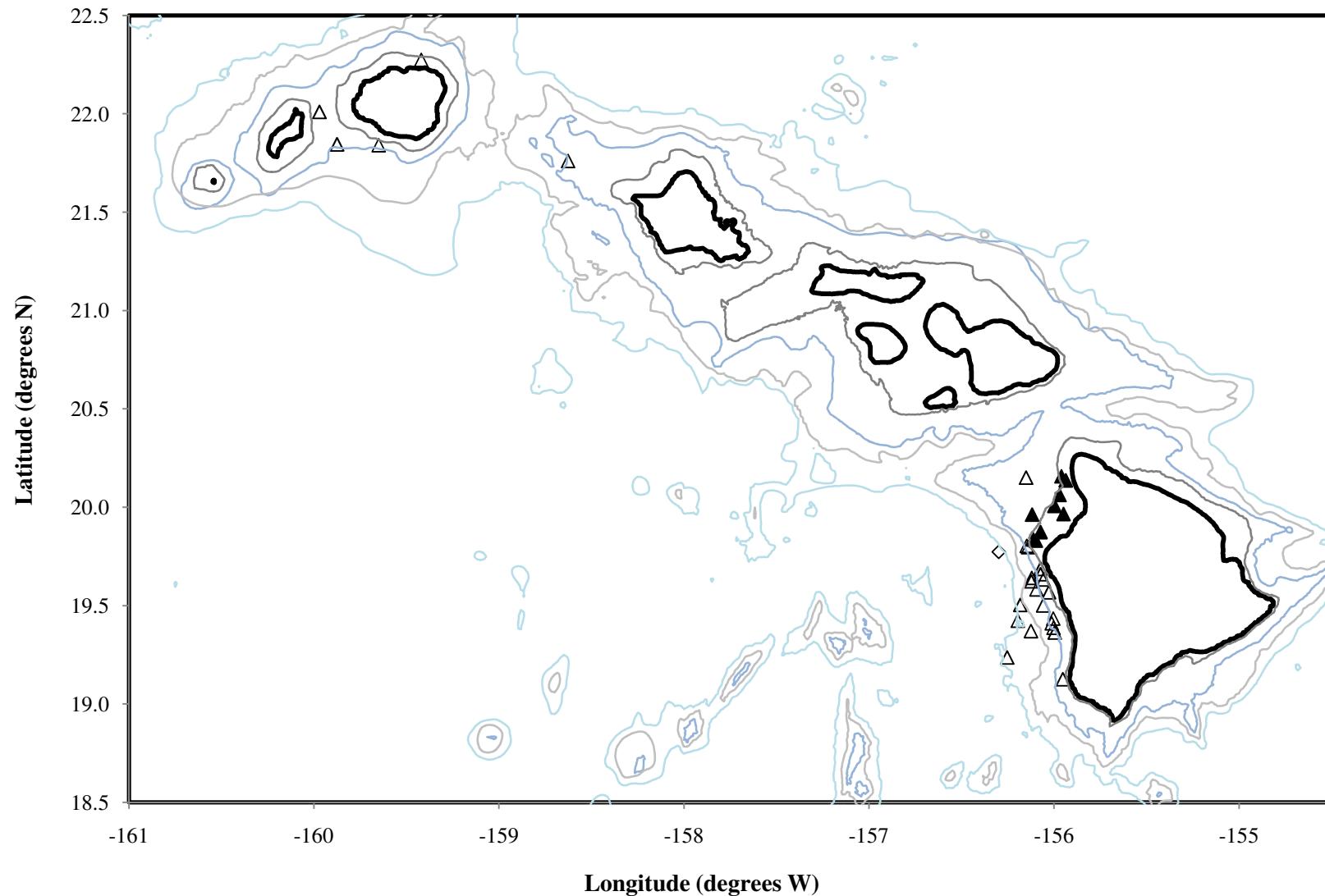


Figure 2.11 Map of melon-headed whale sightings from dedicated surveys between 2002 and 2009. Filled triangles show encounter locations with the Hawai'i resident population, unfilled triangles show encounter locations with the Main Hawaiian Islands population, and the unfilled diamond represents the encounter with the group that did not link to either population. Depth contours are 500 m, 1,000 m, 3,000 m, and 4,000 m.

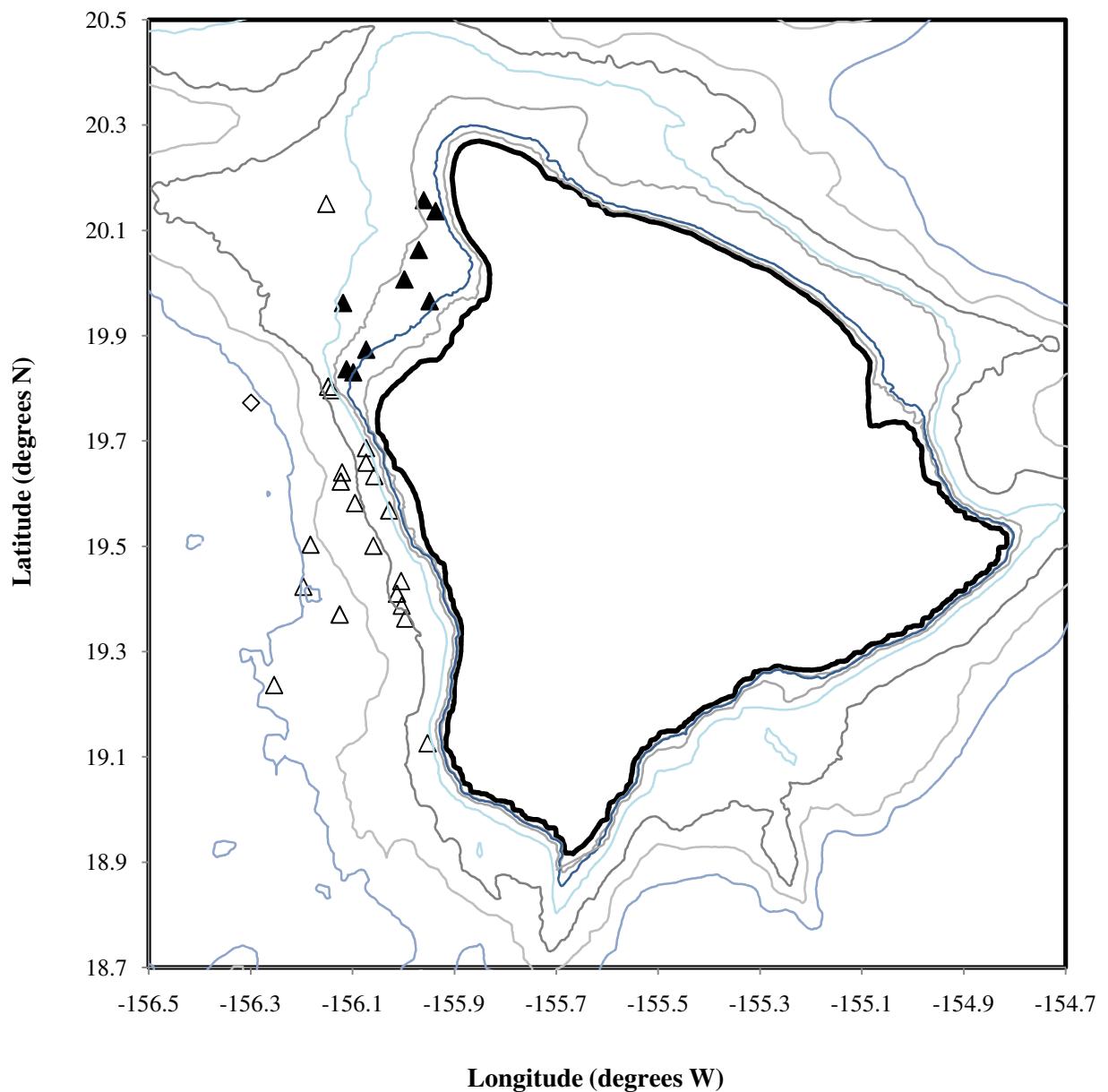


Figure 2.12 Map of melon-headed whale sightings from dedicated surveys between 2002 and 2009 off the island of Hawai'i. Filled triangles show encounter locations with the Hawai'i resident population, unfilled triangles show encounter locations with the Main Hawaiian Islands population, and the unfilled diamond represents the encounter with the group that did not link to either population. Depth contours are 100 m, 200 m, 500 m, 1,000 m, 2,000 m, 3,000 m, and 4,000 m.

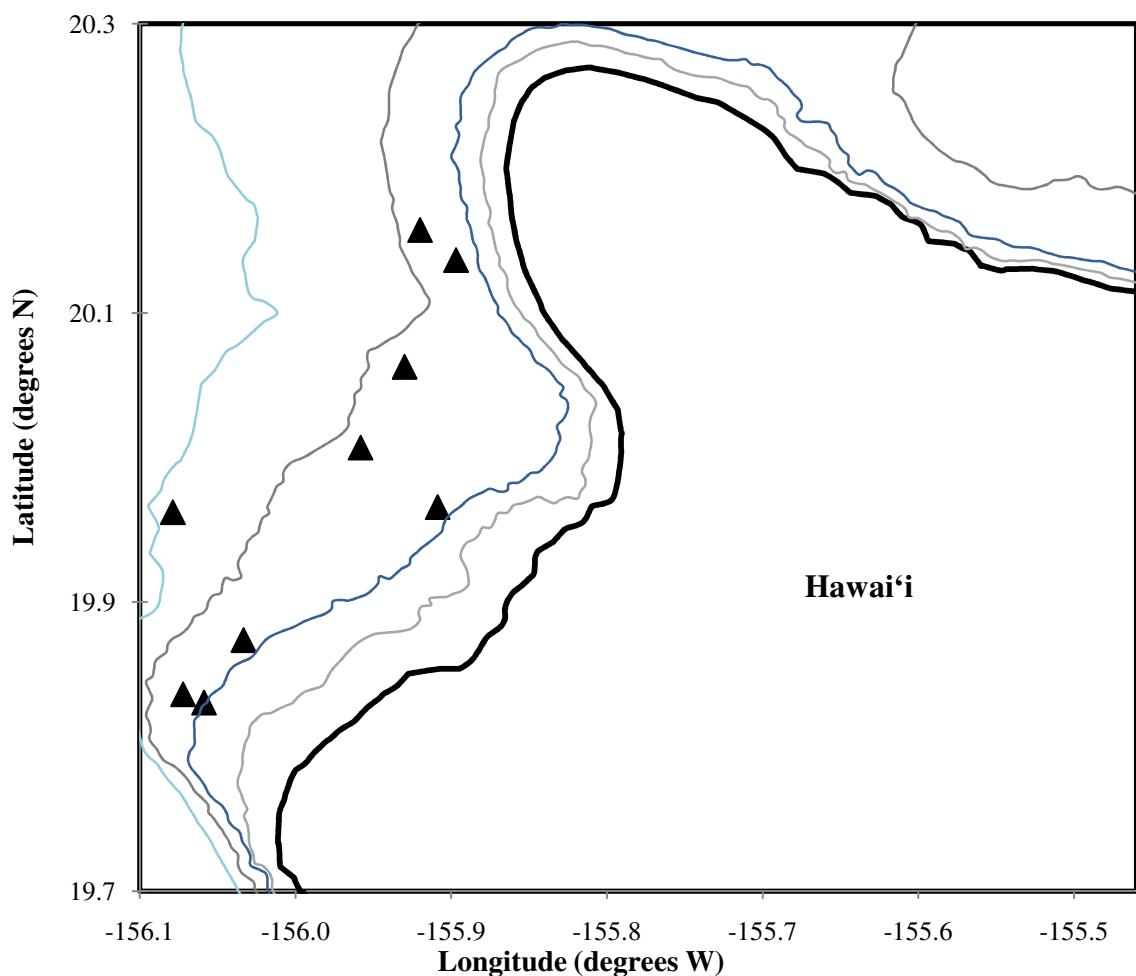


Figure 2.13 Sightings of the resident population of melon-headed whales from directed surveys between 2002 and 2009 off the northwest region of the island of Hawai'i. Depth contours are 100 m, 200 m, 500 m, and 1,000 m.

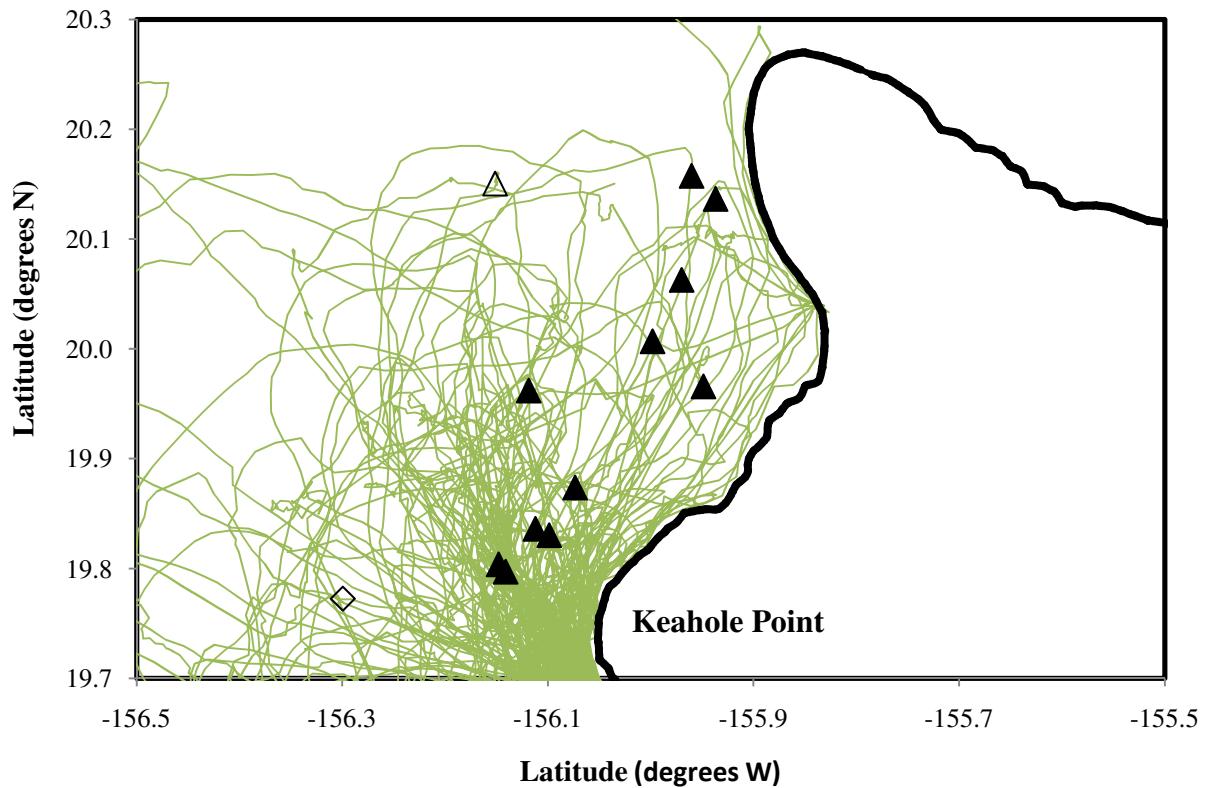


Figure 2.14 Effort tracklines (green) and sightings of melon-headed whales from directed surveys between 2002 and 2009 north of Keahole Point, Hawai‘i. Filled triangles show encounter locations with the Hawai‘i resident population, unfilled triangles show encounter locations with the Main Hawaiian Islands population, and the unfilled diamond represents the encounter with the group that did not link to either population.

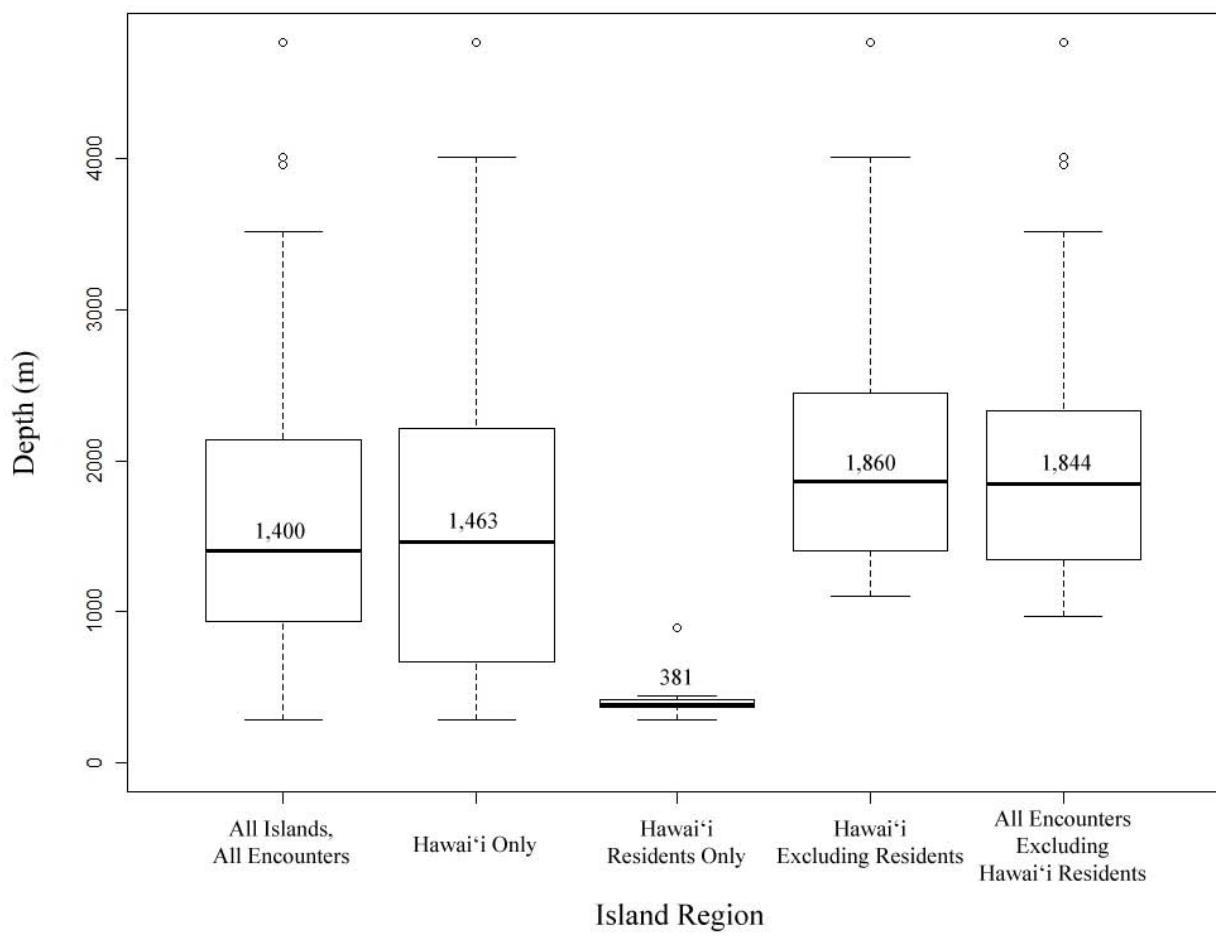


Figure 2.15 Box plots showing distribution of depths of melon-headed whale encounters by area and for Hawai'i residents and all others only. Middle bold lines show median values, upper and lower lines of boxes encompass the spread of data from the first to the third quartile, and upper and lower horizontal lines show minimum and maximum depth values unless outliers are present (◦), in which the horizontal line is defined as the third quartile plus 1.5.

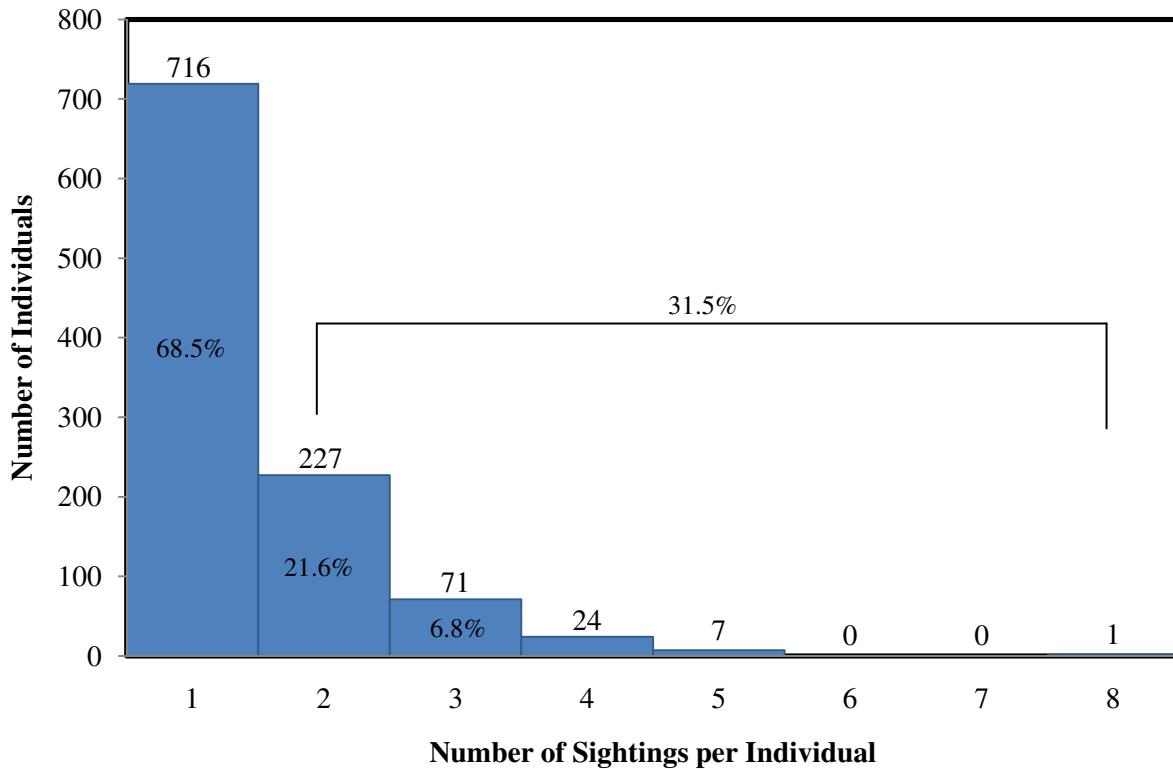


Figure 2.16 Frequency of individual melon-headed whale sightings around the Main Hawaiian Islands from 2002 – 2009 using well-photographed (rated 3 or 4), distinctive (rated 3 or 4) individuals.

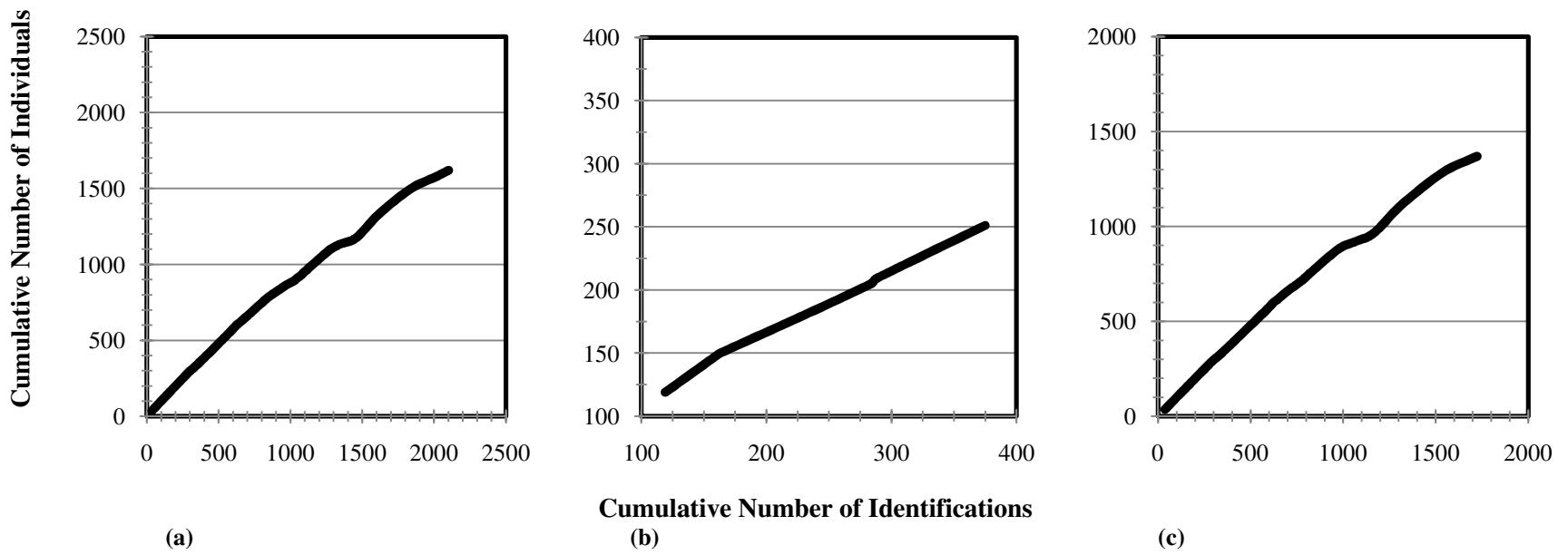


Figure 2.17 Discovery curves showing the cumulative number of individuals per cumulative number of identifications (a) for all individual melon-headed whales in all encounters (b) for all individual melon-headed whales in the Hawai‘i resident population, and (c) for all individual melon-headed whales with the exception of the Hawai‘i resident population. The lack of an asymptote on each discovery curves indicates that the number of identifications is not a true representation of the population.



(a)

(b)

Figure 2.18 Long term re-sighting of individual melon-headed whale HPe1579. This animal was first seen in April 1986, re-sighted in September 1996, February 2005, July 2006, and most recently in December 2008, a total length of time spanning more than 22 years. This individual is part of the Hawai‘i resident population of melon-headed whales occurring off the northwest side of the island of Hawai‘i. Photo (a) ©Dan McSweeney, Wild Whale Foundation; (b) ©Cascadia Research Collective, Russ Andrews.



(a)

(b)

Figure 2.19 Cataloged individuals HPe0739 and HPe0740; both first seen off Hawai‘i on September 17, 2004, re-sighted together off Hawai‘i on April 19, 2008 (a), and re-sighted together again off Kaua‘i on June 29, 2008 (b). At least 65 animals were re-sighted with an animal it had previously been photographed associating with. Photos ©Cascadia Research Collective; (a) Daniel Webster (b) Annie Douglas.

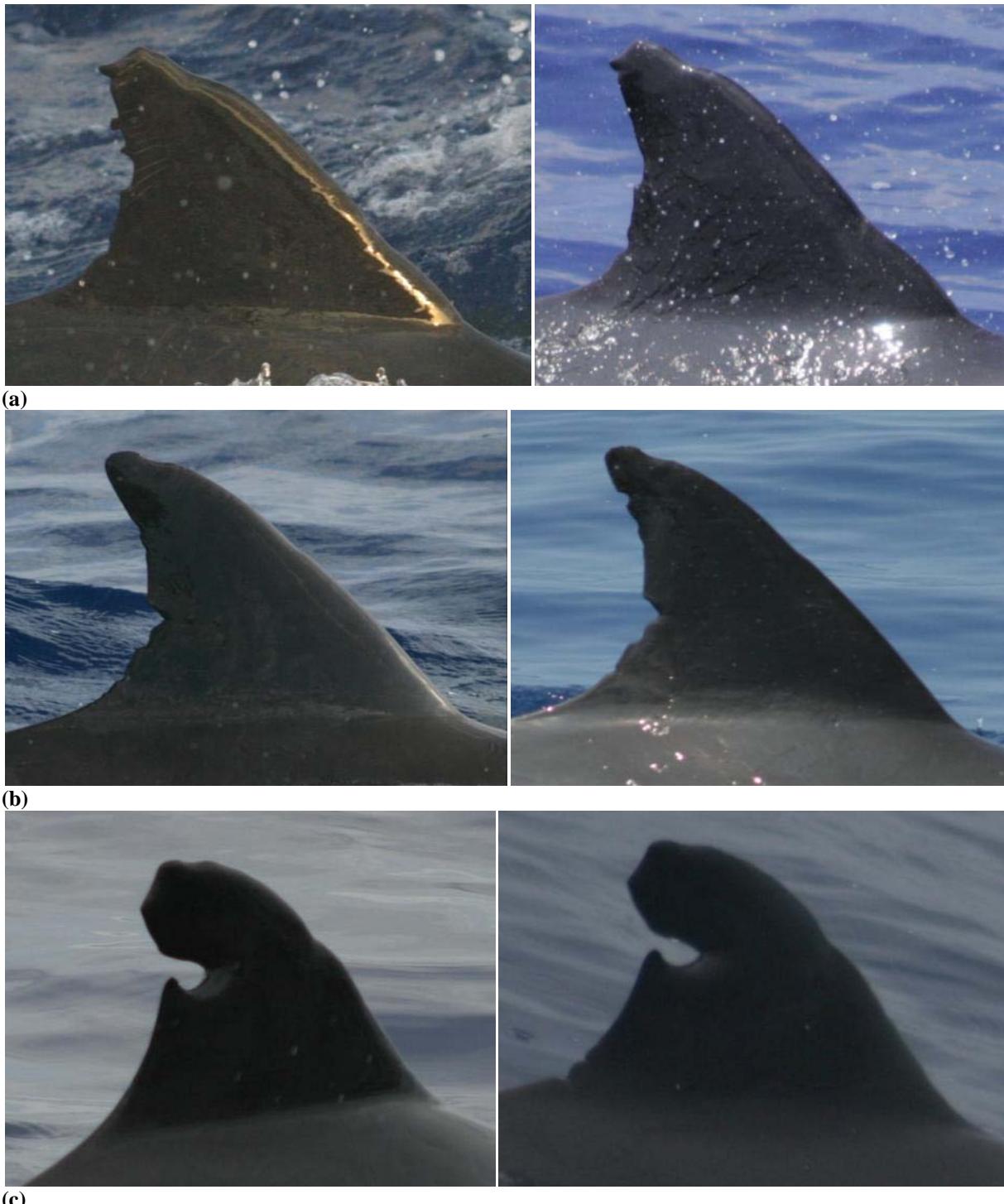


Figure 2.20 (a) Example of an individual who became less distinct with mark changes (catalog no. HIPe0452): photo on the left taken September 17, 2004; photo on the right taken three and a half years later on April 19, 2008. (b) Example of an individual who became more distinct with mark changes (catalog no. HIPe0456): photo on the left taken September 17, 2004; photo on the right taken three and a half years later on April 19, 2008. (c) Example of an individual who became more distinct with mark changes (catalog no. HIPe0657): photo on the left taken February 2, 2005; photo on the right taken one and a half years later on March 26, 2006. All photos ©Cascadia Research Collective; (a) Allan Ligon, Dan McSweeney (b) Allan Ligon, Greg Schorr (c) Greg Schorr (d) Daniel Webster.

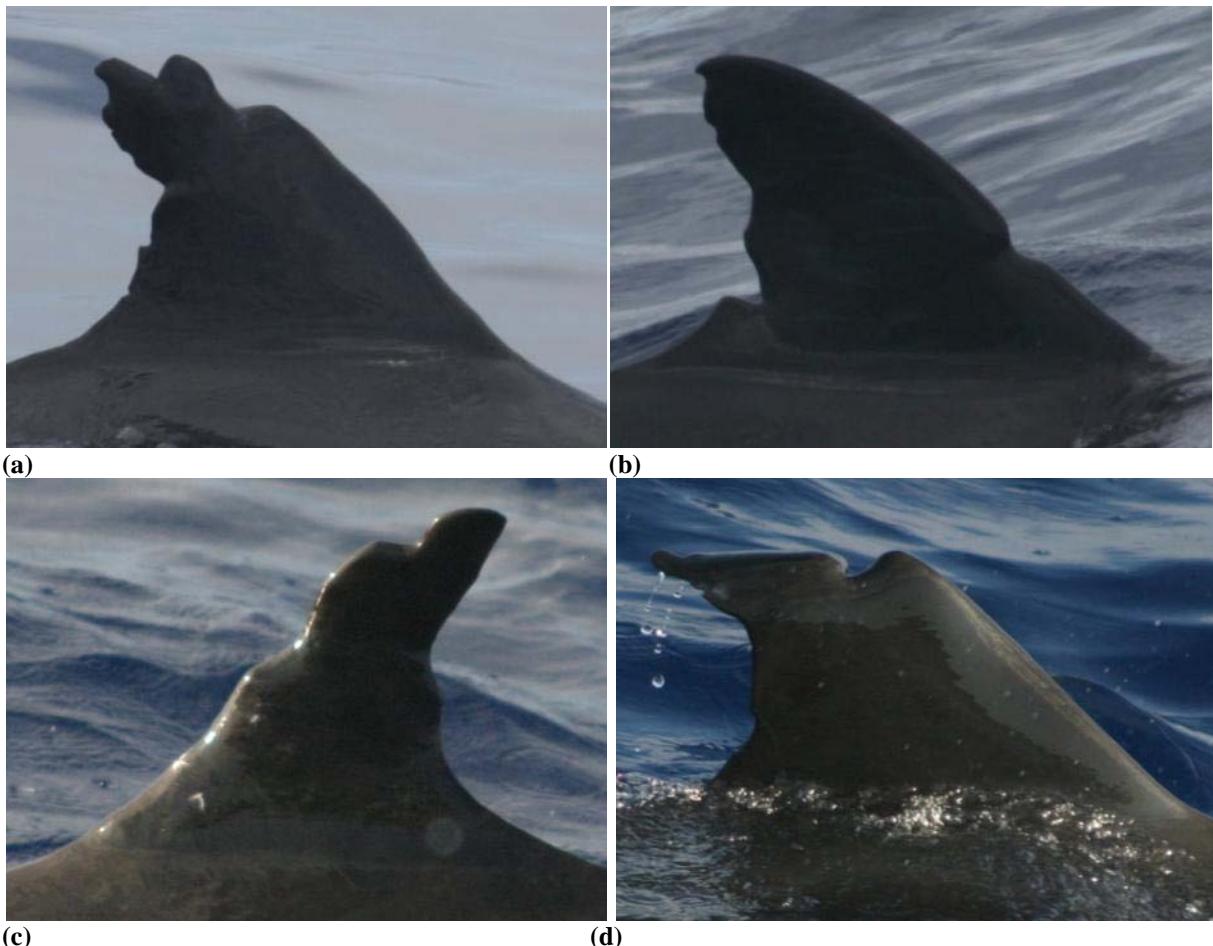


Figure 2.21 (a) – (d) Examples of dorsal fin injuries of melon-headed whales likely due to line or rope entanglement. (a) Multiple leading edge notches and corresponding trailing edge notches suggest multiple wraps from line or rope (catalog no. HIPe1032). (b) This individual's dorsal has healed and left a deep leading edge notch combined with a deep trailing edge notch (catalog no. HIPe1511). (c) It is possible that multiple wraps around the dorsal fin caused the several prominent leading edge notches on this animal (catalog no. HIPe0526). (d) The top third of this dorsal fin was partially separated from the fin, causing the remaining portion to bend slightly (catalog no. HIPe0515). Photos ©Cascadia Research Collective; (a) and (b) Greg Schorr, (c) and (d) Allan Ligon.



Figure 2.22 (a) – (b) Examples of probable line entanglement scars across individual melon headed whales in Hawai'i. **(a)** The deep groove can be seen towards the head of this individual (catalog no. HIPe1264). **(b)** While the grooves are shallower on this animal (catalog no. HIPe1466), indication that the line or rope wrapped around the body are evident by the markings both dorsally and laterally. Photos ©Cascadia Research Collective; **(a)** Annie Douglas **(b)** Daniel Webster.

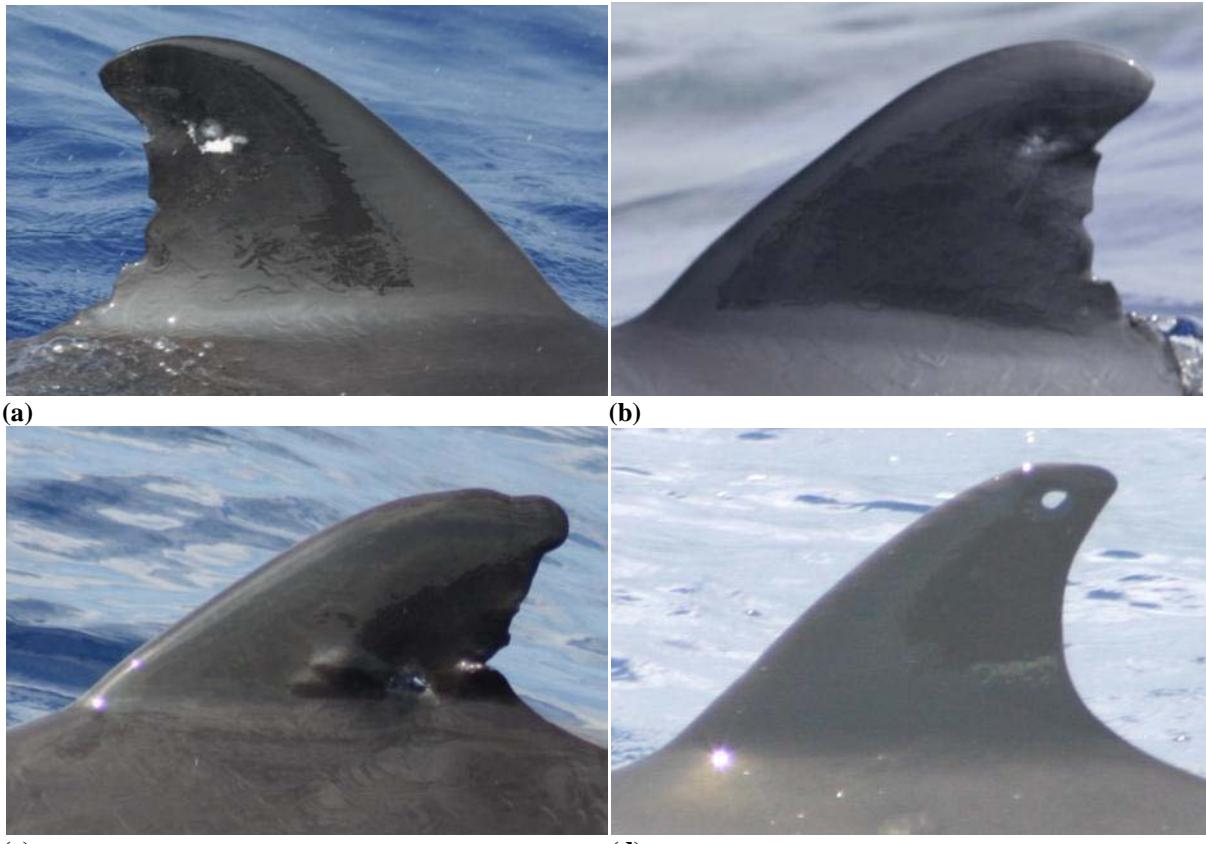


Figure 2.23 (a) – (d) Examples of dorsal fin injuries of melon-headed whales potentially caused by bullet wounds; (a) and (b) are right/left sides of the same individual (catalog no. HIPe0603), (c) entry wound is in the process of healing on this individual (catalog no. HIPe1593), (d) fully healed opening in dorsal fin (catalog no. HIPe0040). Photos ©Cascadia Research Collective; (a) Allan Ligon (b) Darren Roberts (c) Robin Baird (d) Alice Mackay.



(b)

Figure 2.24 Bodily injuries to melon-headed whale that were probably caused by a propeller strike (catalog no. HIPe1136). Rake marks are also visible on this animal and can be used to note the difference in distances between marks. Photos ©Cascadia Research Collective, Darren Roberts.

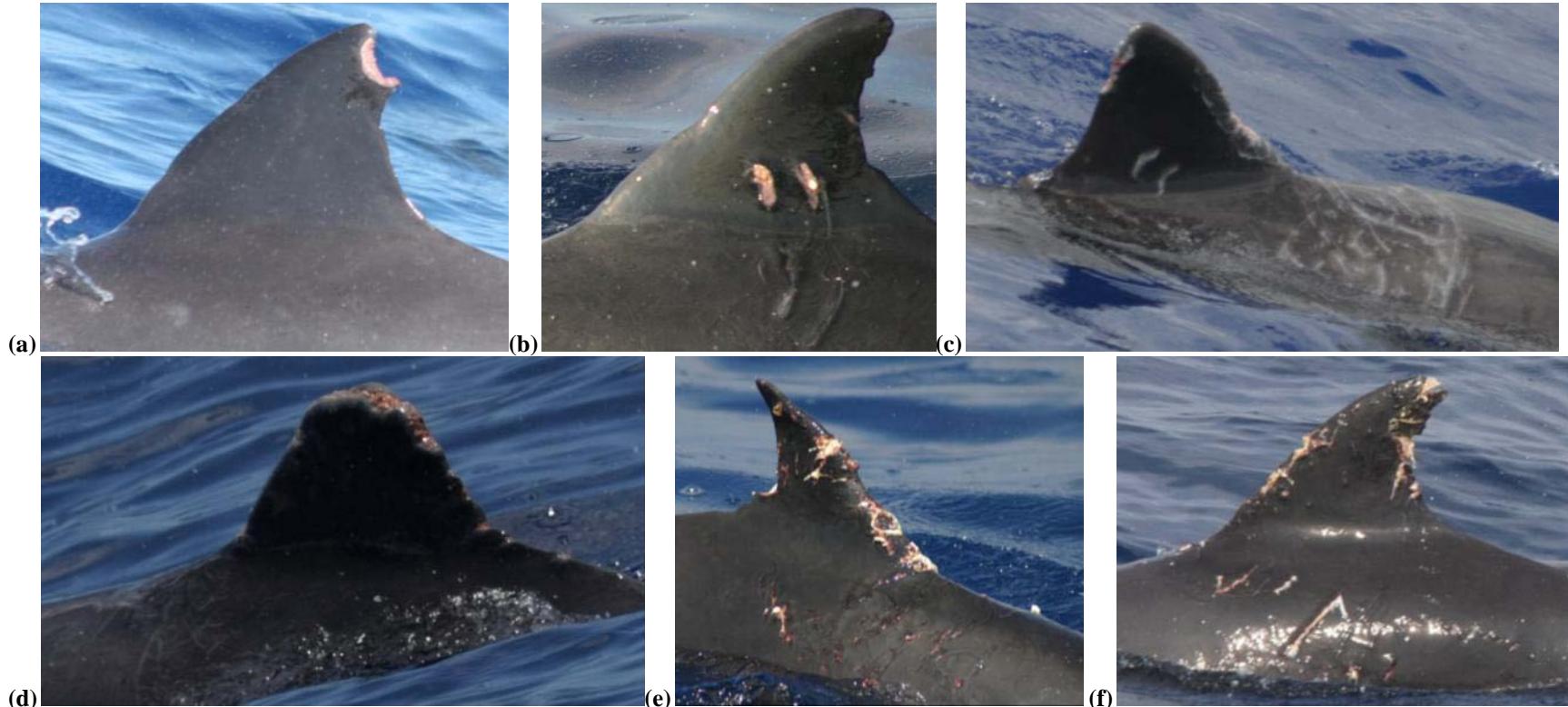


Figure 2.25 Other noteworthy dorsal injuries. (a) The injury to the top of this dorsal fin may have been the result of a shark bite (catalog no. HIPe1215). (b) Deep wounds are gorged into the side of this fin, possibly from a shark bite (catalog no. HIPe0486). (c) Despite the presence of more extensive injuries on this individual (catalog no. HIPe0493), the two parallel markings across the dorsal fin are similar in appearance to injuries from the previous animal, HIPe0486, although further along in the healing process. (d) Severe, but unknown injuries (catalog no. HIPe1054) (e) Severe, but unknown injuries (catalog no. HIPe0129) (f) Severe injuries, possibly from shark bites (no catalog no.). Notice the top of the dorsal fin has been sliced down the center. Photos ©Cascadia Research Collective; (a) Robin Baird (b) Allan Ligon (c) Robin Perrtree (d) Annie Douglas (e) Allan Ligon (f) Daniel Webster.



Figure 2.26 Female melon-headed whale with neonatal calf. Fetal folds are present on the calf. Note that the mother has a dorsal wound that might be attributable to a shooting injury. Photo ©Cascadia Research Collective, Dan McSweeney.



(a)



(b)

Figure 2.27 (a) HPe0657 and presumed calf, March, 2006. (b) HPe0657 and a larger presumed calf, October, 2009. Photos ©Cascadia Research Collective (a) Daniel Webster (b) Greg Schorr.

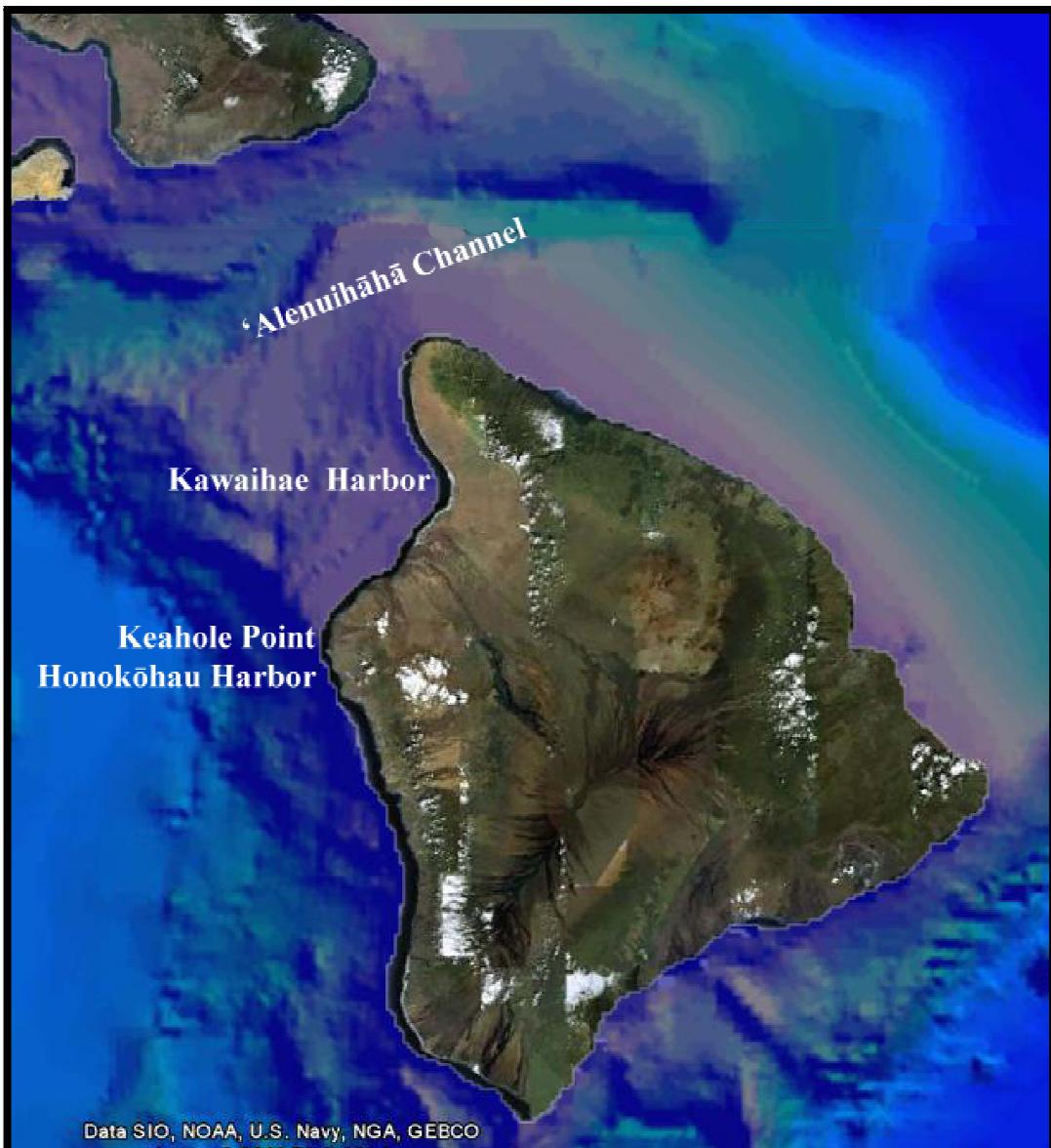


Figure 2.28 Bathymetry of the waters off the island of Hawai'i. The waters off the northwestern region are much shallower than due west of the island. The deeper grooved channel between Hawai'i and Maui/Kaho'olawe is the 'Alenuihāhā Channel, an area of high winds and higher productivity with a maximum depth of ~1,900 m. Also depicted are the two main boat harbors on the leeward side of the island, Kawaihae and Honokōhau, as well as the westernmost point of the island, Keahole Point. From Google Earth, ©2009 Europa Technologies.



Figure 2.29 Individual melon-headed whales from the resident population interacting with humpback whales off the northwestern side of the island of Hawai‘i. (a) Three melon-headed whales emerge in front of a humpback whale. (b) A lone melon-headed whale surfaces in front of a humpback whale (catalog no. HIPe1512). Photos ©Cascadia Research Collective; (a) Mark Deakos (b) Daniel Webster.

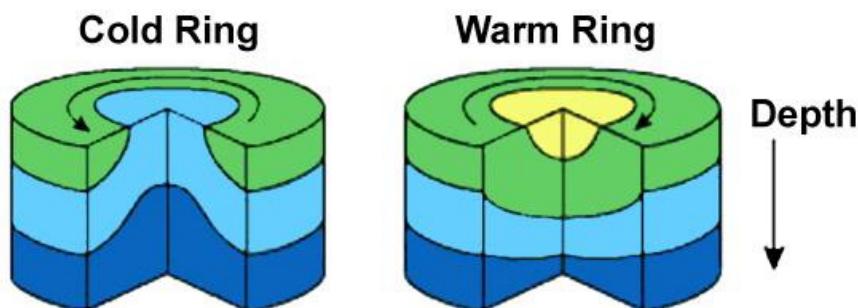


Figure 2.30 Cyclonic cold ring and anticyclonic warm ring eddies. Cyclonic eddies are associated with upwelling and increased sea surface height and anticyclonic eddies are associated with downwelling and decreased sea surface height. From www.disc.sci.gsfc.nasa.gov.

Literature Cited

- Andrews, K.R., Karczmarski, L., Au, W.W.L., Richards, S., Vanderlip, C.A., Toonen, R.J. 2006. Patterns of genetic diversity of the Hawaiian spinner dolphin (*Stenella longirostris*). Atoll Research Bulletin 543: 65-73.
- Andrews, K.R., Karczmarski, L., Au, W.W.L., Rickards, S.H., Vanderlip, C.A., Bowen, B.W., Gordon Grau, E., Toonen, R.J. 2010. Rolling stones and stable homes: Social structure, habitat diversity, and population genetics of the Hawaiian spinner dolphin (*Stenella longirostris*). Molecular Ecology 19:732-748.
- Anonymous. 2006. Supplement to the 2002 Rim of the Pacific (RIMPAC) Programmatic Environmental Assessment. Available from http://www.nmfs.noaa.gov/pr/pdfs/permits/rimpac_ea.pdf (accessed August 2006).
- Anonymous. 1997. Fishery council hears of dolphin deaths, sea turtle slaughter, bird bycatch. Environment Hawai'i 8: 8.
- Baird, R.W., McSweeney, D.J., Webster, D.L., Gorgone, A.M., Ligon, A.D. 2003. Studies of odontocete population structure in Hawaiian waters: results of a survey through the main Hawaiian Islands in May and June 2003. Report prepared under Order No. AB133F-02-CN-0106 from the National Oceanic and Atmospheric Administration, Western Administrative Support Center, 7600 Sand Point Way N.E., Seattle, WA 98115 USA.
- Baird, R.W., McSweeney, D.J., Bane, C., Barlow, J., Salden, D.R., Antoine, L.K., LeDuc, R.G., Webster, D.L. 2006. Killer whales in Hawaiian waters: information on population identity and feeding habits. Pacific Science 60:523-530.
- Baird, R.W., Webster, D.L., Mahaffy, S.D., McSweeney, D.J., Schorr, G.S., Ligon, A.D. 2008a. Site fidelity and association patterns in a deep-water dolphin: rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian Archipelago. Marine Mammal Science 24: 535-553.
- Baird, R.W., Gorgone, A.M., McSweeney, D.L., Salden D.R., Deakos M.H., Ligon A.D., Schorr, G.S., Barlow, J., Mahaffy, S.D. 2008b. False killer whales (*Pseudorca crassidens*) around the Main Hawaiian Islands: long-term site fidelity, inter-island movements, and association patterns. Marine Mammal Science 24: 591-612.
- Baird, R.W., Schorr, G.S., Webster, D.L., McSweeney, D.J., Hanson, M.B., Andrews, R.D. 2008c. Multi-species cetacean satellite tagging to examine movements in relation to the 2008 Rim-of-the-Pacific (RIMPAC) naval exercise. A quick look report on the results of tagging efforts undertaken under Order No. D1000115 from the Woods Hole Oceanographic Institution.
- Baird, R.W., Gorgone, A.M., McSweeney, D.J., Ligon, A.D., Deakos, M.H., Webster, D.L., Schorr, G.S., Martien, K.K., Salden, D.R., Mahaffy, S.D. 2009. Population structure of

island-associated dolphins: evidence from photo-identification of common bottlenose dolphins (*Tursiops truncatus*) in the Main Hawaiian Islands. *Marine Mammal Science* 25: 251-274.

Baird, R.W. 2009. A review of false killer whales in Hawaiian waters: biology, status, and risk factors. Report prepared for the U.S. Marine Mammal Commission under Order No. E40475499.

Barlow, J. 2006. Cetacean abundance in Hawaiian waters estimated from a summer/fall survey in 2002. *Marine Mammal Science* 22: 446-464.

Baumann-Pickering. 2009. Species identification and measurement of activity in odontocete species off Palmyra Atoll by Acoustic Monitoring. PhD dissertation. Eberhard Karls Universität Tübingen.

Benoit-Bird, K.J. and Au, W.W.L. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology* 53: 364-373.

Borgatti, S.P. 2002. Netdraw Network Visualization. Analytic Technologies: Harvard, MA.

Brownell, R.J., Ralls, K., Baumann-Pickering, S., Poole, M.M. 2009. Behavior of melon-headed whales near oceanic islands. *Marine Mammal Science* 25: 639-658.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., Pollock, K.H. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph* 5: 437pp.

Burnham, K. P. and Anderson, D.R. 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach* (488pp). New York: Springer-Verlag.

Calambokidis, J., Steiger, G.H., Straley, J.M., Herman, L.H., Cechio, S., Salden, D.R., Urban R., J., Jacobsen, J.K., Ziegesar, O.V., Balcomb, K.C., Gabriele, C.M., Dahleim, M.E., Uchida, S., Ellis, G., Miyamura, Y., Ladron de Guevara P., P., Yamahuchi, M., Sato, F., Mizroch, S.A., Schlender, L., Rasmussen, K., Barlow, J. 2001. Movements and structure of the Humpback whale in the North Pacific. *Marine Mammal Science* 17: 769-794.

Calambokidis, J., Falcone, E.A., Quinn, T.J., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Matilla, D., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urbán R., J., Weller, D., Witteveen, B.H., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggins, J., Maloney, N. 2008. SPLASH: Structure of population levels of abundance, and status of humpback whales in the North Pacific. Final report for contract AB133F-03-RP0078.

- Chivers, S.J., Baird, R.W., McSweeney, D.J., Webster, D.L., Hedrick, N.M., Salinas, J.C. 2007. Genetic variation and evidence for population structure in eastern North Pacific false killer whales (*Pseudorca crassidens*). Canadian Journal of Zoology, 85: 783-794.
- Doty, M.S., and Oguri, M. 1956. The island mass effect. Journal du Conseil-Conseil International pour l'Exploration de la Mer 22: 33-37.
- Fromm, D.M., Mobley, J.R.J., Martin, S.W., Nachtigall, P.E. 2006. Analysis of melon-headed whale aggregation in Hanalei Bay, July 2004. Journal of the Acoustical Society of America; Meeting of the Acoustical Society of America. 120: 3266.
- Gilmartin, M., and Revelante, N. 1974. The island mass effect on the phytoplankton and primary production of the Hawaiian Islands. Journal of Experimental Marine Biology and Ecology 16: 181-204.
- Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. Reports of the International Whaling Commission Special Issue 8: 253-281.
- Hammond, P.S. 1990. Capturing whales on film-estimating cetacean population parameters from individual recognition data. Mammal Review 20: 17-22.
- Herman, L.M. and Antinoja, R.C. 1977. Humpback whales in the Hawaiian breeding water: population and pod characteristics. Scientific Reports of the Whales Research Institute (Tokyo) 29: 59-85.
- Hiby, A.R. and Hammond, P.S. 1989. Survey techniques for estimating current abundance and monitoring trends in abundance of cetaceans. In G. P. Donovan (Ed.), The Comprehensive Assessment of Whale Stocks: The Early Years. Cambridge: International Whaling Commission.
- Huggins, J., Baird, R.W., Webster, D.L., McSweeney, D.J., Schorr, G.S., Ligon, A.D. 2005. Inter-island movements and re-sightings of melon-headed whales within the Hawaiian Archipelago. In Abstracts of the 16th Biennial Conference on the Biology of Marine Mammals, San Diego, CA, December 2005.
- Karczmarski, L., Würsig, B., Gailey, G., Larson, K.W., Vanderlip, C. 2005. Spinner dolphins in a remote Hawaiian atoll: social grouping and population structure. Behavioral Ecology 16: 675-685.
- Kiszka, J., Pelourdeau, D., Ridoux, V. 2008. Body scars and dorsal fin disfigurements as indicators of interaction between small cetaceans and fisheries around the Mozambique Channel Island of Mayotte. Western Indian Ocean Journal of Marine Science 7: 185-193.
- Knowlton, A.R., Kraus, S.R. 2001. Mortality and serious injury of northern right whales (*Eubalaena glacialis*) in the western North Atlantic Ocean. Journal of Cetacean Research and Management Special Issue 2: 193-208.

- Kuljis, B.A. 1983. Porpoise/fisheries interactions within the Hawaiian Islands. Southwest Fisheries Science Center Administrative Report H-83-19C. 16 pp.
- Larsen, F. and Hammond, P.S. 2004. Distribution and abundance of west Greenland humpback whales (*Megaptera novaeangliae*). Journal of Zoology, London, 263: 343-358.
- Lebreton, J.-D., Burnham, K. P., Clobert, J., Anderson, D. R. 1992. Modeling survival and testing biological hypotheses using marked animals. A unified approach with case studies. Ecological Monographs 62: 67-118.
- McSweeney, D.J., Baird, R.W., Mahaffy, S.D. 2007. Site fidelity, associations, and movements of Cuvier's (*Ziphius cavirostris*) and Blainvilles's (*Mesoplodon densirostris*) beaked whales off the island of Hawai'i. Marine Mammal Science 23: 666-687.
- McSweeney, D.J., Baird, R.W. Mahaffy, S.D., Webster, D.L., Schorr, G.S. 2009. Site fidelity and association patterns of a rare species: pygmy killer whales (*Feresa attenuata*) in the Main Hawaiian Islands. Marine Mammal Science 25: 557-552.
- Miyazaki, N., Fuhise, Y., Iwata, K. 1998. Biological analysis of a mass stranding of melon-headed whales (*Peponocephala electra*) at Aoshima, Japan. Bulletin of the National Science Museum Series A (Zoology), Tokyo 24: 31-60.
- Mobley, J.R., Spitz, S.S., Forney, K.A., Grotfendt, R., Forestell, P.H. 2000. Distribution and abundance of odontocete species in Hawaiian waters: preliminary results of 1993-98 aerial surveys. Southwest Fisheries Science Center Administrative Report LJ-00-14C.
- Mobley, J.R., Martin, S.W., Fromm, D., Nachtigall, P.E. 2007. Lunar influences as possible cause for simultaneous aggregations of melon-headed whales in Hanalei Bay, Kauai, and Sasanhaya Bay, Rota. In Abstracts of the 17th Biennial Meeting on the Biology of Marine Mammals, Society for Marine Mammalogy, Cape Town, South Africa.
- Mullin, K.D. 1994. First sightings of melon-headed whales (*Peponocephala electra*) in the Gulf of Mexico. Marine Mammal Science 10: 342-248.
- Norris, K.S., Würsig, B., Wells, R.S., Würsig, M. 1994. The Hawaiian Spinner Dolphin. Berkeley University Press, Berkeley, CA. 408 pp.
- Perrin, W. F. 1976. First record of the melon-headed whale, *Peponocephala electra*, in the eastern Pacific, with a summary of world distribution. Fishery Bulletin 74: 457-458.
- Perryman, W.L., Au, D.W.K, Leatherwood, S., Jefferson, T.A. 1994. Melon-headed whale *Peponocephala electra* Gray, 1846. Pages 363-386 in S. H. Ridgway and R. Harrison, eds. Handbook of Marine Mammals. Vol. 5. The First Book of Dolphins. Academic Press, London, U.K.

- Pollock, K.H., Nichols, J.D., Brownie, C., Hines, J.E. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs*, 107: 1-97.
- Pollock, K.H. and Alpizar-Jara, R. 2005. Classical Open-population Capture-Recapture Models. In S.C. Amstrup, T.L. McDonald & B.F.J. Manly (Eds.), *Handbook of Capture-Recapture Analysis* (pp. 313). Princeton, NJ: Princeton University Press.
- Pradel, R., Choquet, R., Lima, M.A., Merritt, J., Crespin, L. *In Press*. Estimating population growth rate from capture-recapture data in the presence of capture heterogeneity. *Journal of Agricultural, Biological, and Environmental Statistics*.
- Reeves, R.R., Stewart, B.S., Clapham, P.J., Powell, J.A. 2002. National Audubon Society Guide to Marine Mammals of the World. Alfred A. Knopf, New York, NY 528pp.
- Seber, G.A.F. 1982. The Estimation of Animal Abundance and Related Parameters. Griffin, London, 2nd edition. 654 pp.
- Schwarz, C. J. and Arnason, A. N. 1996. A general methodology for the analysis of capture–recapture experiments in open populations. *Biometrics* 52: 860–873.
- Schorr, G.S., Baird, R.W., Webster, D.L., McSweeney, D.J., Hanson, M.B., Polovina, J., Andrews, R.D. 2009. Satellite tagging of melon-headed whales (*Peponocephala electra*) in Hawai‘i reveals widely dispersed movement patterns. In Abstracts of the 18th Biennial Conference on the Biology of Marine Mammals, Quebec, October 2009.
- Scott, E.M., Mann, J., Watson-Capps, J.J., Sargeant, B.L., Connor, R.C. 2005. Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour* 142: 21-44.
- Seki, M.P., Bidigare, R.R., Lumpkin, R., Polovina, J.J., Kobayashi, D.R., Flament, P., Foley, D.G. 2001. Mesoscale cyclonic eddies and pelagic fisheries in Hawaiian waters. *Oceans* 3: 1590-1594.
- Shallenberger, E.W. 1981. The Status of Hawaiian Cetaceans. Report MMC-77/23 to the Marine Mammal Commission under contract MM7ACo28, NTIS PB82-109398, 79 pp.
- Southall, B.L., Braun, R., Gulland, F.M.D., Heard, A.D., Baird, R.W., Wilkin, S.M., Rowles, T.K. 2006. Hawaiian melon-headed whale (*Peponocephala electra*) mass stranding event of July 3-4, 2004. NOAA Technical Memorandum NMFS-OPR-31.
- Taylor, B.L., Chivers, S.J., Larese, J., Perrin, W.F. 2007. Generation length and percent mature estimates for IUCN assessments of cetaceans. Administrative Report No. LJ-07-01. National Marine Fisheries Service, Southwest Fisheries Science Center.
- Van Waerebeek, K.V., Baker, A.N., Félix, F., Gedamke, J., Iñiguez, M., Sanino, G.P., Secchi, E., Sutaria, D., van Helden, A., Wang, Y. 2007. Vessel collisions with small cetaceans

worldwide and with large whales in the southern hemisphere, an initial assessment. Latin American Journal of Aquatic Mammals 6: 43-69.

Viña, J., Borrás, C., Gambini, J., Sastre, J., Pallardó, F.V. 2005. Why females live longer than males? Importance of the upregulation of longevity-associated genes by oestrogenic compounds. FEBS Letters 579: 2541-2545.

Watkins, W.A., Daher, M.A., Samuels, A., Gannon, D.P. 1997. Observations of *Peponocephala electra*, the melon-headed whale, in the southeastern Caribbean. Caribbean Journal of Science 33: 34-40.

Wells, R.S. and Scott, M.D. 1990. Estimating bottlenose dolphin population patterns from individual identification and capture-recapture techniques. Reports of the International Whaling Commission Special Issue 12: 407-415.

Wells, R.S. and Scott, M.D. 1997. Seasonal incidence of boat strikes on bottlenose dolphins near Sarasota, Florida. Marine Mammal Science 13: 475-480.

White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: 120–138.

Wilson, B., Hammond, P.S., Thompson, P.M. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. Ecological Applications 9: 288-300.

Woodworth, P., Schorr, G.S., Baird, R.W., Webster, D.L., McSweeney, D.J., Hanson, M.B., Andrews, R.D., Polovina, J.J. *Submitted*. Eddies as offshore foraging grounds for melon-headed whales (*Peponocephala electra*). Manuscript.

Appendix 1

HAWAII ENCOUNTER, TAGGING AND BIOPSY SHEET

RECORD ITEMS IN BOLD IMMEDIATELY								<i>Record items in italics at end of encounter</i>				
Date:	/	/	Start time	(24 h clock)	Species	Sight.	#	<i>On/Off Effort</i>	Cue	<i>see below</i>		
Boat	Obs initials	Obs. Pos. (Upper/Lower, P/S/F/B)	Recorder initials	Sea Cond. <i>(Beaufort/swell, e.g., B2/S2')</i>	Group size:	<i>MIN</i>	/	<i>BEST</i>	/	<i>MAX</i>		
Wpt # (first seen)	Wpt # (@ group)	Lat/Long: (@ start)	(Lat/Long always in dd.ddddd/ddd.ddddd)								Behav. <i>(see below)</i>	DOT:
Group Envelope: <i>(e.g., 100 x 400 m)</i>	% group observed: <i>(close enough to note remoras, cookie-cutter (CC) wounds, neonates etc)</i>		# w/CC wounds	% w/CC wounds:	<i>#wounds/individual</i>							
End Time:				Lat/Long:	Wpt#	Behav:	DOT:					
#Fish vessels	Reason for Leaving: <i>(see below)</i>		Neonates:	yes / no / unk	#:	YOY:	yes / no / unk	#:	<i>(circle)</i>			
Prey/fecal samples	Sight# for other research boat <i>(type/# - details on effort log)</i>	other species present - Species: <i>(use separate data sheet for other species)</i>	Sighting # other species		Mixed group	Yes / No						
Photographer initials	/ Camera	/ Card # s	/ Start/end frames	/ End blank								
Photographer initials	/ Camera	/ Card # s	/ Start/end frames	/ End blank								
Photographer initials	/ Camera	/ Card # s	/ Start/end frames	/ End blank								
Photographer initials	/ Camera	/ Card # s	/ Start/end frames	/ End blank	Total # photos							
PERMIT INFO:												
Primary Permit	# reacting overall approach <i>(SWFSC/RWB)</i>	avoidance distance (m)	#approach <1 body length									
Biopsy Permit	# attempts:	# hits:	# samples	# target animal	# non-target							
Tagging Permit	# suction attempts	# dart attempts	# tagged	# taken incidental								
AT END OF DAY												
Distance to shore (from GPS)	km	Closest Landmark (from GPS, include island)	Start depth	m	Distance from 1 ^a seen (from GPS)	m						
Notes:												
<p><i>Cue=ORV, Other Research Vessel; SBF, Splash, Blow, Fin; FV, Fishing Vessel; Birds; Radio call. Observer = individual(s) who spots animals. Behavior e.g., travel, mill, social, feeding, rest. DOT =direction of travel. YOY =young of year. Reason for Leaving:1. Group Lost; 2. Group Not Approachable; 3. Continuing Search, some samples/IDs; 4. Continuing Search, all IDd; 5. Continuing search, low priority; 6. higher priority species seen; 7. Weather/time of day. Please cross out or write NA in all spaces not used. For "Notes", record presence of remoras, group size changes, audio recordings (duration etc), description of un-identified species, other samples collected, types of fishing vessels, behavior, etc. Rev. 8 Nov 2008</i></p>												

Appendix 2

ENCOUNTER SUMMARY							
MHI = Main Hawaiian Islands, Unk = Unknown, RWB = Robin W. Baird, CRC = Cascadia Research Collective, DJM = Daniel J. McSweeney, MFR = Michael F. Richlen, SWFSC = Southwest Fisheries Science Center, PIFSC = Pacific Islands Fisheries Science Center							
Date	Days since last encounter	Island	Population	Encounter duration	Group size (best)	# photographic frames	Source
04-Oct-02	N/A	Hawai'i	MHI	3:43	300	177	RWB
10-May-03	218	Kaua'i	MHI	0:28	50	16	RWB
29-May-03	19	O'ahu	MHI	1:14	190	131	RWB
05-Jun-03	7	Kaua'i	MHI	2:13	200	527	RWB
13-Oct-03	130	Hawai'i	MHI	0:43	17	45	CRC
13-Oct-03	0	Hawai'i	MHI	1:35	275	501	CRC
14-Oct-03	1	Hawai'i	MHI	0:41	275	126	CRC
17-Sep-04	339	Hawai'i	MHI	4:29	300	1206	CRC
22-Sep-04	5	Hawai'i	Unk	1:09	240	359	CRC
03-Oct-04	11	Hawai'i	MHI	1:05	120	447	CRC
03-Oct-04	0	Hawai'i	MHI	1:56	220	642	CRC
06-Oct-04	3	Hawai'i	MHI	0:09	300	53	CRC
22-Nov-04	47	Hawai'i	MHI	1:29	450	827	CRC
25-Nov-04	3	Hawai'i	MHI	1:05	250	1106	CRC
22-Jan-05	58	Hawai'i	MHI	1:37	420	1003	CRC
24-Jan-05	2	Hawai'i	MHI	1:40	800	868	CRC
26-Jan-05	2	Hawai'i	MHI	1:46	525	450	CRC
02-Feb-05	7	Hawai'i	Resident	1:38	550	929	CRC
07-Aug-05	186	Hawai'i	MHI	Unk	Unk	120	SWFSC
25-Mar-06	230	Hawai'i	Resident	Unk	Unk	144	DJM
26-Mar-06	1	Hawai'i	Unk	0:16	4	29	CRC
26-Mar-06	0	Hawai'i	Resident	3:48	350	957	CRC
30-Mar-06	4	Hawai'i	Resident	0:46	210	650	CRC
31-Mar-06	1	Hawai'i	Resident	0:10	4	94	DJM
31-Mar-06	0	Hawai'i	Unk	0:13	1	74	CRC
29-May-06	59	Hawai'i	MHI	Unk	Unk	129	DJM
24-Jul-06	56	Hawai'i	Resident	1:46	465	2272	CRC
05-Oct-07	438	Hawai'i	MHI	Unk	Unk	28	MR
08-Oct-07	3	Hawai'i	MHI	Unk	28	7	MR
08-Feb-08	123	Hawai'i	MHI	Unk	Unk	620	PIFSC
19-Apr-08	71	Hawai'i	MHI	4:41	325	2265	CRC
25-Apr-08	6	Hawai'i	MHI	1:22	182	840	CRC
30-Apr-08	5	Hawai'i	MHI	2:07	140	1301	CRC
25-Jun-08	56	Kaua'i	MHI	2:45	220	2045	CRC
29-Jun-08	4	Kaua'i	MHI	1:30	340	2108	CRC
30-Jun-08	1	Kaua'i	MHI	0:48	340	2129	CRC
02-Jul-08	2	Hawai'i	MHI	0:50	300	655	CRC
10-Dec-08	161	Hawai'i	MHI	2:10	335	2732	CRC
10-Dec-08	0	Hawai'i	Resident	0:34	525	847	CRC
15-Dec-08	5	Hawai'i	Resident	0:43	425	1952	CRC
25-Apr-09	131	Hawai'i	MHI	1:17	25	134	CRC
02-Oct-09	160	O'ahu	MHI	Unk	Unk	2981	PIFSC
11-Oct-09	9	O'ahu	MHI	Unk	Unk	1265	PIFSC
12-Oct-09	1	O'ahu	MHI	Unk	Unk	1615	PIFSC
15-Oct-09	3	O'ahu	MHI	Unk	Unk	1358	PIFSC
21-Oct-09	6	Hawai'i	Resident	0:45	50	1418	CRC
09-Dec-09	49	Hawai'i	Resident	0:26	160	609	CRC